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PACIFIC SCIENCE

A QUARTERLY DEVOTED TO THE BIOLOGICAL AND PHYSICAL SCIENCES OF THE PACIFIC REGION

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Reproduction, Life History, and Larval Ecology of the California Xanthidae, the Pebble Crabs

JENS W. KNUDSEN[1]

THIS STUDY is concerned with the reproduction, life history, and larval ecology of the California Xanthidae, the pebble crabs. The Brachyura of the west coast of North America are not well known with reference to their behavior and ecology. Because of its economic importance, the edible crab, *Cancer magister* Dana, has been made the subject of a series of studies by Weymouth (1917), Weymouth and MacKay (1934, 1936), and MacKay (1942). The only studies of economically unimportant species are those of Wells (1940) on the pinnotherid crabs of Puget Sound, and Hiatt (1948) on the lined shore crab, *Pachygrapsus crassipes* Randall. The latter study is concerned primarily with ecology and behavior, and its thoroughness makes it a pattern for similar studies. The present paper is the partial result of a study on the family Xanthidae made by the writer while at the Allan Hancock Foundation, University of Southern California.
The writer is grateful to Dr. John S. Garth and Dr. Norman T. Mattox for their guidance in this work.

The xanthid crabs of California are common but seldom seen members of the lower intertidal-zone fauna, found along protected rocky beaches. Their superficial resemblance to beach pebbles and their ability to "play dead" make them an interesting group to study. Because of their similarity, the scope of this paper has been broadened to cover the four major species found locally, rather than just one species. Thus, *Lophopanopeus leucomanus leucomanus* (Lockington), *Lophopanopeus bellus diegensis* Rathbun, *Paraxanthias taylori* (Stimpson), and *Cycloxanthops novemdentatus* (Lockington) are discussed collectively as the major California Xanthidae. Information concerning the reproduction and life history of this group is almost totally lacking. This is also true, with regard to larval ecology, for all Brachyura of western North America.

REPRODUCTION

Sexual Dimorphism and Maturity

The only distinct, sexually dimorphic characteristics of significance in the California Xanthidae are found in the abdomen of mature and submature specimens. The chelipeds of some male crabs are said to be larger than those of the female of the same species. There is considerable variation of length-width ratios of chelae among the local xanthid crabs, but there is no strongly marked trend towards dimorphism. It is generally true that the largest specimens are males. However, if the life span of the male and female crab is approximately the same, then the size difference is easily explained by the work of Hiatt (1948: 165) with *Pachygrapsus crassipes*. Hiatt demonstrated that the normal molt cycle of female crabs is interrupted by periods of egg bearing, and that a longer time is thus required for the female to reach a size equal to a male. If this applies to the Xanthidae as well, then the larger size of the male is not sexual dimorphism, but is due to a normal interruption of the female molt cycle. The abdomen, however, shows definite dimorphic trends, and at the time of maturity differs distinctly in male and female specimens.

In taxonomic work, as well as in natural history, it is often very useful to know if a particular specimen or size-class is mature. Gonad study is impractical because (1) the specimen is destroyed, (2) the sex organs may be dormant at the time of year which the specimen is collected, making determination impossible, and (3) the individual would be of no further use in a natural history study. Therefore, it is useful to have certain external signs with which mature specimens may be separated from im-

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mature. Seventy-five female xanthid crabs were dissected in the month of June to correlate size, gonad development, and abdominal characteristics. An additional 178 females were examined and measurements were taken on 63 of the premature to mature size range. These data will be presented for each species.

Cycloxanthops novemdentatus: This species shows signs of sexual dimorphism beginning at the 6.5 millimeter (carapace width) size class. Prior to this the male and female abdomen are alike, composed of seven segments, the third being the widest segment, while the sixth segment is less than two-fifths the width of the second. From about 6.5 millimeters carapace width the abdominal segments of the female distal to the third segment broaden with each additional molt. From the data given for this species (Table 1) it can be seen that there are two distinct classes, immature and mature, and a transitional submature class.

The immature specimens are those females in which the gonads are undeveloped and lack ova. External signs of this are as follows: (1) the third abdominal segment is the widest of all segments; (2) the marginal abdominal "hair"

TABLE 1

A SURVEY OF MATURE AND IMMATURE FEMALE *Cycloxanthops novemdentatus**

WIDTH IN MM.	WIDEST AB. SEG.	LATERAL "HAIR"	LOCK	SPERMATHECA	CONDITION OF OVARIES	CONDITION OF EGGS
17.2	3	1/8	×	0	undeveloped	—
18.0	3	1/8	×	0	undeveloped	—
19.1	3	1/8	×	0	undeveloped	—
19.2	3	1/8	×	0	undeveloped	—
19.4	3	1/8	×	0	undeveloped	—
20.8	3–4	5/8	—	0	somewhat developed	—
22.5	3–4	7/8	—	0	somewhat developed	—
23.5	3	1/4	×	0	undeveloped	—
24.0	3	1/4	×	0	undeveloped	—
24.2	3	1/4	×	0	undeveloped	—
25.0	3	1/4	×	0	undeveloped	—
25.8	3	1/4	×	0	undeveloped	—
26.0	3	1/4	×	0	undeveloped	—
26.2	3	1/4	×	0	undeveloped	—
26.4	3	1/4	×	0	somewhat developed	—
27.0	3	1/4	×	0	undeveloped	—
28.5	3–4	1/2	×	0	somewhat developed	—
30.0	3–5	1/2	×	0	somewhat developed	—
31.2	3–5	3/4	×	0	somewhat developed	—
32.8	4–5	1	—	large	ripe, gravid	—
32.9	4–5	1	—	large	ripe, gravid	lg. blastomeres
33.0	3–5	1	—	medium	ripe, gravid	—
33.3	3–5	1	—	large	ripe, gravid	—
34.0	4–5	1	—	medium	ripe, gravid	lg. blastomeres
34.5	4–5	1	—	medium	ripe, gravid	new
35.5	4–5	1	—	medium	somewhat developed	—
36.8	4–5	1	—	large	ripe, gravid	new
37.0	4–5	1	—	large	ripe, gravid	—
37.5	4–5	1	—	large	ripe, gravid	—
38.0	4–5	1	—	large	ripe, gravid	—
38.5	4–5	1	—	medium	ripe, gravid	new
40.0	4–5	1	—	medium	ripe, gravid	—
41.0	4–5	1	—	large	ripe, gravid	lg. blastomeres
42.8	4–5	1	—	medium	ripe, gravid	—
52.3	4–5	1	—	large	ripe, gravid	—

* The lateral abdominal hair length is given as a fraction of the third abdominal segment length; ×, present; —, absent; O, spermatheca empty; lg., spermatheca large, full of sperm; med., spermatheca of medium size, with some sperm.

is 25 per cent or less than the length of the third abdominal segment; (3) the sixth abdominal segment is narrower than the second in young, but immature females; (4) the pleopods are sparsely provided with "hairs"; and (5) the lock mechanism is present. The lock mechanism is typical of male crabs of this species, and consists of a pair of cup-shaped pockets on the distal-lateral margins of the sixth abdominal segment, and a pair of protuberances projecting forward from the fifth thoracic sternite which lies in union with the sixth abdominal segment. When the abdomen is "closed," the cups of the sixth segment fit over the protuberances of the sternite and serve to lock the abdomen in place. The last abdominal segment is free, and is extended for defecation without lowering the entire abdomen. The protuberances of the sternite are the most conspicuous evidence of this mechanism. Generally the maximum carapace width of the immature female is 28.5 millimeters.

Submature or transitional females have well-developed ovaries but generally lack developing ova. The morphological changes from the preceding stages are as follows: (1) abdominal segments three and four are of nearly equal width; (2) the lateral "hair" on the sixth segment is almost 50 per cent as long as the third abdominal segment; (3) the pleopods are more fully developed; and (4) the lock mechanism is generally present. The size of this stage ranges between 28.5 and 33.0 millimeters.

The fully mature female *Cycloxanthops novemdentatus* is about 33.0 millimeters wide or wider, and has fully developed, gravid ovaries (in season). Externally these specimens can be determined by the following features: (1) abdominal segments four and five are the widest; (2) the lateral "hair" of the sixth segment is about equal in length to the third abdominal segment; (3) the sixth segment is wider than the third; (4) the pleopods are very full in appearance; (5) the lock mechanism is lacking entirely; and (6) the groove in the sternum occupied by the abdomen is proportionally shallower and wider than in the immature or male condition.

About 4 per cent of the females examined had a carapace width of 19.2 to 21.5 millimeters, but had all of the characteristics of a mature female. Normally female *Cycloxanthops novemdentatus* are not ovigerous until June in southern California, and the individual young take about the same length of time to develop, probably two years. The small but mature females are probably hatched early in April, and thus are large enough in the following year to be influenced by the warm temperatures of late summer. Hence, the secondary sex characteristics are brought on abnormally early.

Hiatt (1948: 198) used the presence of sperm in the vas deferens as a criterion of maturity in male *Pachygrapsus crassipes*. The writer examined preparations from 15 *Cycloxanthops novemdentatus*, several other xanthid crabs, and several *Pachygrapsus crassipes* (within the mature size range), but concluded that the poor results obtained were not worth the destruction of additional specimens. A study of the external genitalia of the male, however, reveals that the intromittent organs are capable only of anterior-posterior movement. Thus successful copulation could not occur except with equal-sized females. In this species the intromittent organs are fully developed when the individual is 19.5 millimeters wide. Just prior to this they appear normal but are shorter than normal. Thus 20-millimeter males are able to copulate with small, mature females. However, the fertility of males in this size-class has not been established.

Paraxanthias taylori: The anatomical features important in determining the maturity of this species are the same as for *Cycloxanthops novemdentatus*. Signs of sexual dimorphism are seen in 6.5 millimeter specimens when the distal abdominal segments of the female begin to broaden with respect to segment three. There is no clear-cut transitional or submature class, in that the morphological features of such a class in this species are too indefinite to be of value.

Immature females which have underdeveloped ovaries are characterized by the following external signs: (1) the third abdominal segment is the widest; (2) the second abdominal segment is wider than the sixth segment; (3) the lateral "hair" on segment six is one half or less the length of the third abdominal segment; (4) and the lock mechanism is always present.

Females of this species mature between the sizes of 11.5 millimeters to 13.5 millimeters. The

wide range in size is probably due to their long breeding season which allows considerable size variation in each year class. Mature specimens have either gravid ovaries, eggs attached to the pleopods, or both. The anatomical changes and signs of a mature female are as follows: (1) the fourth abdominal segment is as wide as or wider than the third segment in the smaller mature specimens, while the fourth and fifth segments are wider than the third segment in older females; (2) the sixth abdominal segment is wider than the second; (3) the lateral "hair" on the sixth and/or seventh segment is equal to the length of the third abdominal segment; (4) the lock mechanism is lacking; and (5) the abdominal groove in the thorax is shallower and broader than in immature stages.

An attempt to analyze the maturity of males of this species and of the genus *Lophopanopeus* also met with little success. In both cases, however, the intromittent organs were fully developed when the male had reached a size somewhat smaller than the minimal size (11.5 mm.) of a mature female.

Lophopanopeus l. leucomanus and *L. bellus diegensis:* These species were studied independently but the data obtained were so similar that both will be discussed together. Sexual dimorphism is evident when the female reaches a size of 4.5 millimeters. This genus evidently matures more quickly in these latitudes than do the other genera, for ovigerous females having a carapace width of only 8.5 to 9.0 millimeters are common. This fact, together with the fact that this genus has the longest breeding season, explains in part its extensive northerly range.

Immature females have the following characteristics: (1) the third abdominal segment is wider than any other; (2) the lateral "hair" on the sixth segment is one-half or less the total length of the third abdominal segment; (3) the pleopods are underdeveloped; and (4) the lock mechanism is always present.

Mature females change in the following way: (1) the fourth abdominal segment is as wide or wider than the third segment; (2) the lateral "hairs" on the last two abdominal segments equal the length of the third segment; (3) the pleopods are fully developed; and (4) the lock mechanism is absent.

Internal and External Genitalia

The anatomical features of the genitalia are the same for the three genera studied, although there are some minor variations in shape and size of such parts as the male intromittent organs. The genitalia of *Cycloxanthops novemdentatus* will be presented as a representative type of the other genera in this study.

The internal genitalia of the male (Fig. 1, A) consist of the testes, which are dorsal to the liver mass and which join medially over the posterior portion of the stomach. From the testes arise two tightly coiled ducts which are the glandular portion of the vasa deferentia and which secrete a fluid which aids in the conduction of sperm. From these coils, the vasa deferentia pass posteriorly, leave the visceral area, and terminate in the coxae of the fifth pair of pereiopods.

The first (Fig. 2, A) and second abdominal appendages are modified to transfer sperm to

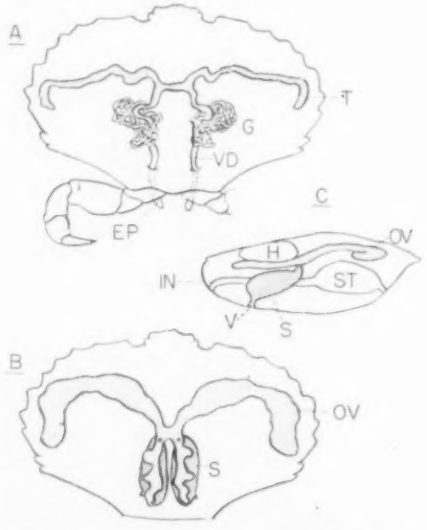


FIG. 1. Internal genitalia: A, Internal genitalia of a male *Cycloxanthops novemdentatus;* B, internal genitalia of a female *Cycloxanthops novemdentatus;* female genitalia, longitudinal view. EP, external papilla; G, glandular portion of the vas deferens; H, heart; IN, intestine; OV, ovary; S, spermatheca; ST, stomach; T, testes; V, vulvae; VD, vas deferens.

the female. The first pair, the intromittent organ, is nearly as long as the abdomen. Each pleopod consists of three segments: the coxopodite, basipodite, and flagellum (after Cochran, 1935: 46). The coxopodite is more or less coalesced with the abdominal segments. The basipodite and flagellum are closely associated and appear as a single unit. Along the median margin of the flagellum of the first pair of pleopods is a canal through which sperm passes, and into which is inserted the flagellum of the second pleopod. The second pleopod moves up and down in the canal during copulation and thus serves as a plunger or pump to force sperm through the canal. There is an external pair of papillae on the coxae of the last pereiopods which transfer sperm from the vasa deferentia to the intromittent organs. These are permanently situated in a funnel-shaped opening on the anterior side of the basipodite of the intromittent organs. Thus, during copulation sperm is conducted through the vasa deferentia, through the external papillae, into the intromittent organs, and there pumped to the terminal end by the second pair of pleopods, and transferred to the vulva of the female.

The internal genitalia of the female are similar to those of the male. There is a pair of ovaries (Fig. 1, B and C) which are U-shaped and lie over the liver anteriorly, and below the heart posteriorly. They unite just behind the dorsal side of the stomach where they give rise to a pair of oviducts. Each oviduct enlarges into a spermatheca as it passes ventrally, narrows again, and terminates in a vulva which opens on the sixth thoracic sternite (Fig. 2, B).

Mating Posture, Time, and Frequency

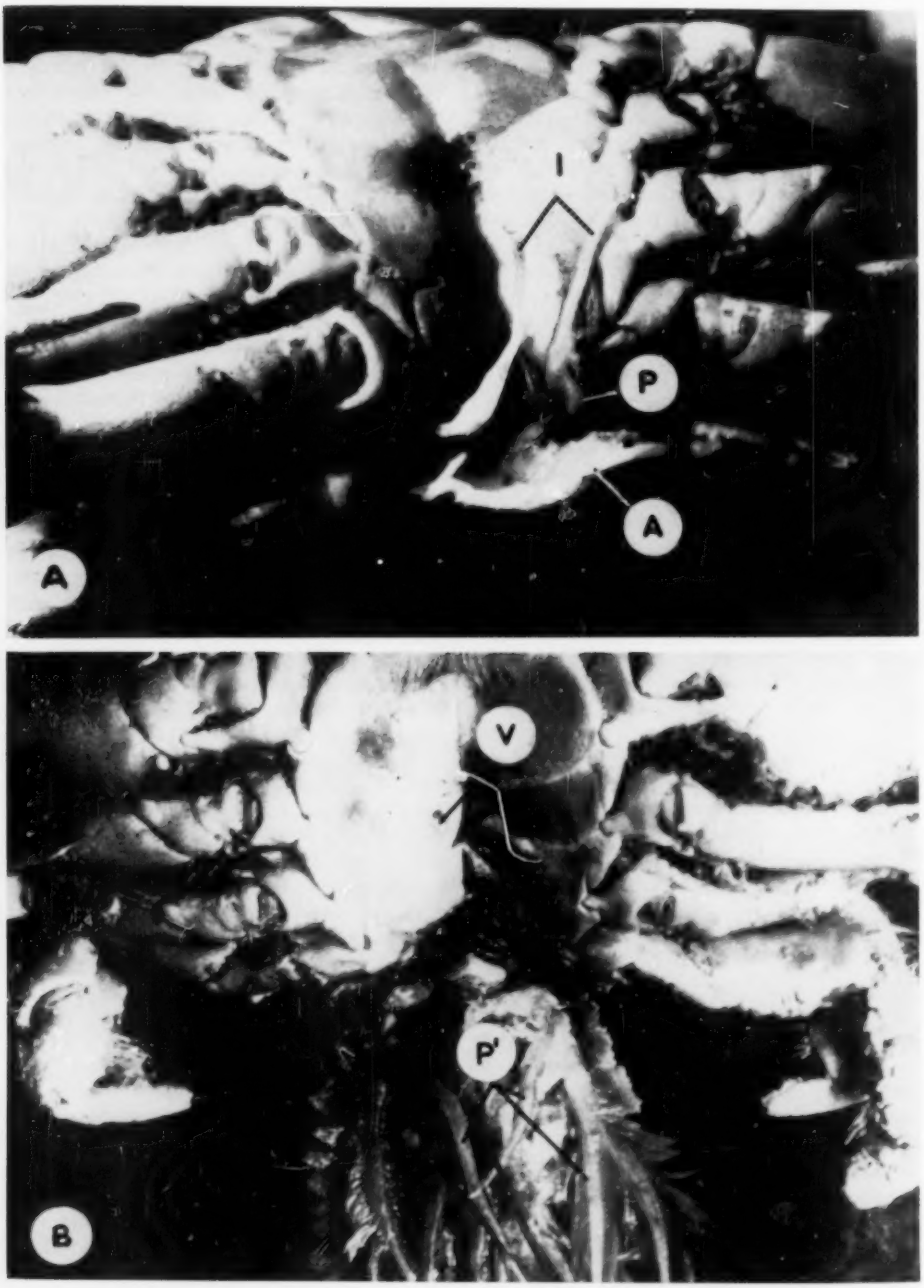
The writer had occasion to see pairs of *Paraxanthias taylori* and of *Lophopanopeus bellus diegensis* in copulation on 12 different occasions in the laboratory. On one of these occasions the entire act was witnessed. There is no prenuptial pairing or courting in the Xanthidae as reported for other crabs by Williamson (1903: 101), Hay (1904: 405), and Churchill (1918: 105). The writer has seen the courting of *Cancer antennarius* on four occasions in the field. During the prenuptial pairing the male of this species carries the slightly smaller female around in his chelae. When disturbed he runs to a hiding place with the female tightly in his grasp. If separated the female is very passive and will offer no defense. The male "courts" the female until she completes ecdysis, at which time they copulate. Two mating pairs of this species were found at Palos Verdes in which the female was completely soft, having just molted. In each intance the crabs were in copulation.

The California Xanthidae breed while in a hard-shell state, and not after molting. The one complete act observed progressed as follows: A male *Paraxanthias taylori* approached a female of this species. The female raised her chelae, which were grasped by the male's chelae, and was lifted above the substratum. Without breaking stride the male pushed the female over backwards and proceeded to straddle her body. The male then lowered his abdomen, catching the female's abdomen with it as he did so. By extending his abdomen under hers, he forced the female to open her abdomen away from her body and thus expose the vulvae. The intromittent organs were lowered automatically with the male's abdomen and were quickly inserted into the vulvae.

In the laboratory, xanthid crabs were seen in copulation for periods up to 3 hours. The male was always dorsal to the female, which is a position typical for most Brachyura, but is unlike that of *Pachygrapsus crassipes* (Hiatt, 1948: 199). Copulation was often repeated by one pair of crabs on several successive days. Forty per cent of the ovigerous females examined had full or partially full spermathecae, which suggests that copulation may not be required for each batch of eggs.

Reproductive Season

There is considerable variation among the major genera of the California Xanthidae in the duration of their reproductive seasons. The writer has observed ovigerous females of *Lophopanopeus l. leucomanus* and of *L. bellus diegensis* collected from February to October inclusive. *Paraxanthias taylori* has the next longest season, with ovigerous females common from April to September. *Cycloxanthops novemdentatus* does not become ovigerous until the middle part of June. Females of this species were collected with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eggs in September, but no later record of egg bearing is available. The local *Lophopanopeus* and *Paraxanthias* remain in the normal tidal range, while ovigerous *Cycloxanthops novemdentatus* migrate to about the minus 3- to 6-foot tide level before extruding their egg masses. Only one ovigerous female of this species has been deposited in the Hancock Foundation collection. Almost all of the ovigerous specimens collected by the writer were obtained by skin diving rather than by collecting on shore. During the reproductive season the sex ratio at the higher tide levels is unbalanced, while in the winter and spring months there is an equal ratio of male and female crabs.

Egg Mass

The egg mass attached to the pleopods of the female varies in proportion to the size of the individual and, to a lesser degree, between different individuals of the same size-class. Table 2 gives the estimated number of eggs carried by 15 xanthid crabs. In each case the eggs were stripped from the pleopods and 300 were counted. The volume of the 300 eggs divided into the total volume multiplied by 300 gave the approximate total number of eggs. In all cases the crabs used were smaller mature individuals rather than older and larger individuals. It can be seen that the total number of eggs is roughly proportional to the size of the individual. Mature *Lophopanopeus* spp. would thus carry from 1,000 to 6,400 eggs within their normal size-range, while an average-sized individual may carry around 3,500 eggs. An average *Paraxanthias taylori* may carry about 21,000 eggs and an average-sized female *Cycloxanthops novemdentatus* about 45,000 eggs.

Egg Extrusion and Attachment

At the time of extrusion of the egg mass the individual eggs pass through the oviduct and into the spermathecae. Then they pass out of the body by means of the vulvae, and drop into a "basket" formed by the abdomen and its appendages. The process of egg extrusion was observed on four occasions, but in each instance the eggs were aborted, and were not fastened to the pleopods. However, this process was essentially the same as when eggs are attached, except that the female crab periodically shook the eggs from her pleopods and allowed them to fall to the floor of the aquarium.

During egg extrusion the female tilts her body backwards and elevates it above the substrate by extending her walking legs beneath her. The abdomen is lowered to about a 50 degree angle below the body plane. The sixth and seventh abdominal segments are turned upward, and together with their marginal "hair" serve to catch the eggs. The exopodites of the four pairs of pleopods are heavily set with "hair" on their anterior and posterior margins. When these are extended laterally they complete the "basket" which receives the eggs. Thus the basi-abdominal segments form the posterior wall, the median segments form the floor, the terminal segments form the anterior wall, and the exopodites form the lateral walls of the egg "basket." Eggs stream from the vulvae and are received by the abdomen. As they do so the endopodites of the pleopods move up and down through the loose egg mass. The endopodites are set with long smooth "hairs" to which the eggs are attached. When a part of an egg mass is examined microscopically it can be seen that there is an umbilical-like thread attached to each egg. This thread is wrapped around and attached to the pleopod "hairs." However, the end of the thread is not attached to the "hairs" but remains free. One of the mysteries, still unsolved, is the origin of this thread, and the method of its attachment to the egg and to the pleopod "hair." Broekhuysen (1936: 277) gives an excellent review of the literature, outlining nine possible answers to the problem, but concludes that the theories are still unsatisfactory for the Brachyura. The present writer observed that there is a sticky consistency to the entire egg mass shortly after being extruded, but he has not had opportunity to study this more fully. This sticky material may be a cement product secreted by the crab, as is the case of the lobster (Herrick, 1895: 48). How-

FIG. 2. External genitalia: A, External genitalia of a male *Cycloxanthops novemdentatus;* B, external genitalia of a female *Cycloxanthops novemdentatus.* A, abdomen; I, intromittent organs; P, second pleopod inserted into the first pleopod; P', pleopods to which the eggs are attached; V, vulvae.

TABLE 2

NUMBER OF EGGS PER MASS OF DIFFERENT SIZES OF XANTHID CRABS

SPECIES	CARAPACE WIDTH	EGGS COUNTED	ESTIMATED TOTAL
L. l. leucomanus	8.5 mm.	300	1,250
L. l. leucomanus	9.2 mm.	300	2,100
L. l. leucomanus	10.0 mm.	300	1,000
L. l. leucomanus	10.0 mm.	300	3,000
L. l. leucomanus	11.5 mm.	300	3,600
L. l. leucomanus	12.0 mm.	300	3,300
L. l. leucomanus	12.5 mm.	300	3,500
L. l. leucomanus	13.5 mm.	300	4,200
P. taylori	15.0 mm.	300	3,800
P. taylori	18.5 mm.	300	6,450
P. taylori	19.0 mm.	300	7,200
P. taylori	29.5 mm.	300	20,300
C. novemdentatus	32.9 mm.	300	22,500
C. novemdentatus	34.5 mm.	300	23,400
C. novemdentatus	38.5 mm.	300	40,680

ever, the eggs are never stuck together after attachment, and are never attached to the exopodites, which are equally as "hairy" as the endopodites. Williamson (1903: 109) suggests that the endopodite "hairs" puncture each egg, and that the "umbilical" thread is then produced by material which streams from the egg. Broekhuysen (1936: 281) has raised many objections to this idea, concluding that it is a physical impossibility.

LIFE HISTORY, STAGES, AND DURATION

The life cycles of four of the most common xanthid crabs in the southern California area were worked out and compared by the writer. Of the four published life cycles of British Columbia Brachyura by Hart (1935: 414), one is of a xanthid crab, *Lophopanopeus bellus bellus* (Stimpson). The data given by Hart compare favorably with those obtained by the writer, thus permitting a discussion which may be applicable to the entire family.

The eggs are attached to the pleopods and there incubated from 25 to 30 days. The female periodically flexes and extends her abdomen as if to allow fresh sea water to wash and aerate the eggs. From time to time the female plucks eggs or other material from the egg mass with her chelae, and conveys this to her mouth. The exact reason for such action is not known, but it may be a method of cleaning the eggs. In the field it was noted that ovigerous females of *Lophopanopeus b. diegensis*, *Lophopanopeus l. leucomanus*, and *Paraxanthias taylori* were often stranded by minus, low tides. These animals make no attempt to enter tidepools a few inches below them, but rather remain in their hiding places. The abdomen of such animals is closed over the egg mass, thus keeping considerable water around the eggs. In the laboratory a tall rock-filled water jar was stocked with ovigerous xanthid females. The sea water was then slowly siphoned out in an attempt to simulate the lowering of tides. *Paraxanthias taylori* and *Lophopanopeus l. leucomanus* did not follow the receding water, but stayed out of water where they finally died. Eggs kept out of water in moist algae up to 6 hours were viable when returned to water. Thus periodic withdrawal of water under normal tidal conditions has no apparent effect on the eggs.

Hatching occurred most frequently at night shortly after dark. Occasionally a few individuals of a given egg mass will hatch during the daylight hours, but these are followed by mass emergence of the other larvae at night. Hatching begins as the egg capsule splits about halfway around, above the dorsal surface of the larva. The larva struggles out of the capsule, dorsal side up, and swims free of the mother crab. During the peak of the hatching period the flexion and extension of the female's abdomen increases very noticeably. With each flexion many larvae are washed away from the egg mass.

The prezoea (the larva just after hatching) has its maxillipeds, antennules, antennae, telson, and spines telescoped. There is no apparent ecdysis between this stage and the first zoea. Rather, the folded extremities are extended by haemocoelic fluid as is the case after normal ecdysis. Hiatt (1948: 204), however, reports true ecdysis after the prezoeal stage in *Pachygrapsus crassipes*. Healthy prezoeae swim for 30 minutes to 2 hours before the expansion is complete. When the larvae are completely expanded they are called zoeae.

There are typically four zoeal stages and one megalops stage in the xanthid life history. The zoeae are pelagic, photopositive forms which

feed on smaller animals or plants. Each zoeal stage resembles the previous one, but shows a marked increase in size. The megalops more closely resembles a crab, having chelae and four pairs of walking legs. This stage settles and molts, thus becoming the first crab stage which resembles the adult. In the laboratory an average of 5 weeks was required to complete the larval stages of the four species. The first zoeal stage lasted from 4 to 6 days. The megalops stage lasted from 7 to 10 days. The first crab stages lasted 13 days, but each stage beyond this required an increase in time for completion.

LARVAL HABITS AND ECOLOGY

Locomotion

The zoea uses two forms of locomotion. The first is a form of directional swimming in which the larva moves in a straight line. Swimming is always carried out in the direction of the dorsal spine so that the body is either in a normal or inverted position (Fig. 3, A, B). The first and second maxillipeds are used as paddles and rapidly move up and down as the larva swims.

FIG. 3. Methods of zoeal locomotion: A, Normal maxilliped locomotion; B, inverted maxilliped locomotion; C_1–C_2, maxilliped-telson or hop-up-and-sink locomotion.

On the distal end of the exopodite of the maxillipeds are four or more plumed natatory "hairs." These "hairs" fan out as the blade of an oar and give the zoea added thrust. After each ecdysis several new natatory "hairs" are added to help propel the additional mass of the zoea.

Weldon (1889: 169) states that steering is effected by means of the telson and abdomen. This may be the case where positive phototaxis is not involved. Mast (1938: 209–216) has shown that photopositive animals with bilaterally located photoreceptors and locomotor organs are affected by the amount of light that each photoreceptor receives. Thus when more light strikes the right eye the left bank of locomotor organs become more active until the body is turned to a point where both eyes are equally illuminated. To test this for the Xanthidae, many zoeae were placed in an 8-inch cylindrical jar in a darkened room. When a light was turned on the larvae swam towards it, but when one light was replaced by a second light 90 degrees away, the larvae turned and swam in that direction. When a light was rotated around the jar the larvae swam in circles in a horizontal plane. When the light was slowly passed over, around and under the jar the larvae swam in vertical circles.

The second form of zoeal locomotion is a random hop-up-and-sink type of movement which follows no definite direction. As a zoea sinks, it draws its abdomen up against its thorax and raises its maxillipeds (Fig. $3C_1$). Simultaneously the abdomen and maxillipeds are thrust downward, resulting in an upward propulsion of the larva (Fig. $3C_2$). The process is repeated so that the zoea remains at approximately the same level in the water column.

Megalops do not use their mouth parts for locomotion but swim by means of pleopods and walk by means of pereiopods. Newly molted megalops are photopositive while older individuals become somewhat photonegative. When swimming, the pereiopods (Fig. 4A) are folded against the body and the abdomen is fully extended. When the megalops turns upward (Fig. 4B) or downward (Fig. 4C) the abdomen is bent up or down, as the elevator of an airplane, to effect the change in direction.

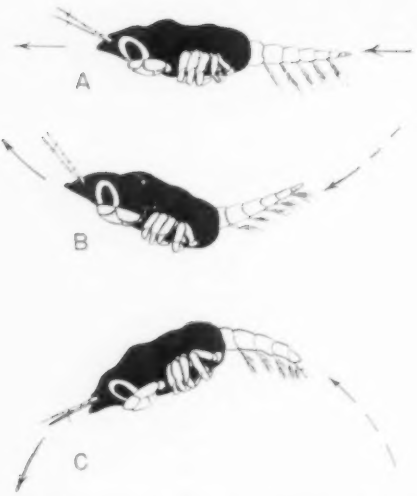

FIG. 4. Locomotion of the megalops stage. See text.

The rate of directional swimming is remarkable. Zoeae placed in a piece of glass tubing 1 inch in diameter and one meter long swam the meter distance in a horizontal plane in 45 to 60 seconds. For this experiment a light was used to maintain the direction of swimming and a wrist watch for timing. These times compare exactly with those recorded by Foxon (1934: 842) for *Galathea, Eupagurus, Pandelus,* and *Porcellana* larvae. Xanthid larvae swam up a 1-meter column in 50 to 60 seconds, while swimming down the column required only 12 to 15 seconds. Xanthid megalops were only timed on one occasion, at shipside while at anchor. The average approximated rate was 2 meters per minute, or about twice the speed of zoeae. Foxon (1934: 843) suggests that the larval swimming rate is sufficient for diurnal migration, which actually does occur (Russell, 1927).

Orientation

Mast (1938: 215) suggests that a portion of the eye functions as a receptor which detects the direction of light. When a light source is present the larvae show no response to gravity as seen above, and as reported by Weldon 1889: 169), Spooner (1933: 395), and Foxon (1934: 838). However, Foxon demonstrates that when light is absent a normal dorsal-up orientation is maintained. Gurney (1902: 475) suggests that the carapace spines play some role in orientation, since statocysts are not present in the zoea. Foxon demonstrated that drugged zoeae, or those with the maxilliped exopodites excised, sank uncontrollably, suggesting awareness and functional exopodites are required also. However, more testing of these theories is necessary.

Food and Feeding Habits

Lebour (1928: 500) states that the natural food of zoeae consists of planktonic organisms, such as diatoms and other microscopic algae, larval and small adult animals. In the laboratory, mixtures of protozoans, turbellarians, diatoms, and other aquarium dwellers were fed to the zoeae. However, the nauplius larva of brine shrimp, *Artemia,* proved to be an excellent source of food for the zoeae. Megalops fed upon *Artemia,* zoeae, and small sessile algae.

Zoeae were observed under the microscope while feeding on nauplius larvae. A zoea catches a nauplius by swimming just a little above it, tilting backward, and dropping down upon it from above. The nauplius is caught between the maxillipeds (which are used for feeding as well as for locomotion) and held by the endopodites. The rostral spine and antennae prevent the nauplius from escaping anteriorly. The abdomen and telson are curled beneath the nauplius, preventing escape posteriorly and ventrally. The mandibles are then in position to feed upon the nauplius. During the feeding process the exopodites of the maxillipeds are used for the locomotion or balance of the zoea.

Ecdysis

In the laboratory the periods of larval ecdysis are the times of the greatest mortality. The molt from the first to the second zoeal stage is the most critical, while the molt and transition from the fourth zoea to the megalops stage is next. During the act of molting a great deal of energy is spent in an attempt to get free of the old "skin." Zoeae which pause to rest generally expand to a point where withdrawal becomes impossible. Larvae in this stage live for a while with the old skin attached to them, but feeding and future molting is generally impossible. Other larvae are so weakened after ecdysis they are

defenseless or unable to capture food, and eventually die.

On a few occasions zoeal ecdysis was seen microscopically. The writer's notes and the examination of zoeae preserved while partially through ecdysis reveal that the process is essentially the same for larvae and adults (Knudsen, 1957: 133–142). The carapace is elevated dorsally above the abdomen. The abdomen and pereiopods are drawn out of the old skin as the new zoea expands upward and backward. As the zoea backs out of the split in the old skin the new dorsal spine is extracted from the old case. The eyes, antennae, and rostral spine are the last parts to be withdrawn. The haemocoelic pressure quickly extends the body to its new size as the molting process is completed. Once free of the old skin the zoea swims away and begins feeding in less than a day's time.

Enemies

To an individual pelagic larval crab, or any other animal, every organism is a possible source of food because it is smaller, or of neutral status because of equal size and strength, or a predator because it is larger. The diatom is generally thought of as the basis of the oceanic food chain. Above this come the tiny, filter-feeding animals, which in turn, serve as food for larger planktonic animals. Thorson (1950: 19) names depredation by other animals as the most important form of wastage of planktonic larvae. The filter feeders, from tiny crustaceans on up to fishes (herring, mackerel) and even whales, probably take the great percentage of larvae.

Obviously the xanthid zoeae are no exception, but fall prey to any stronger or larger predator. In the laboratory zoeae and megalops fed frequently on other zoeae. Many first zoeae were seen to eat the dorsal spine of other living first zoeae. When *Artemia* larvae became too large they too preyed on the zoeae. Copepods experimentally placed in culture jars also took a toll of zoeae.

Mortality of Larvae

Table 2 gave approximate numbers of eggs produced at one time by various sized females. An investigation of the gonads and spermathecae of ovigerous females suggests that more than one egg mass is carried per year. Judging from the length of the breeding season, it appears that *Lophopanopeus* and *Paraxanthias* produce more than two egg masses each year. Thus a 40-millimeter female *P. taylori* may produce up to 120,000 eggs per year.

There is no direct method of measuring the mortality of pelagic larvae. Thorson (1950: 12–19) states that food conditions, temperature conditions, metamorphosis, unfavorable current transport, and predators are the sources of waste of pelagic larvae. Where commercial records are kept for a species for a long period of time some estimate of the total adult population, the yearly spawn, and the larval mortality can be made. However, if the entire population of a species remains relatively constant over a long period of years, then, barring short-term fluctuations, the following supposition can be made: only one pair of F-1 individuals produced throughout the life span of one breeding pair reaches maturity and reproduces. Thus the annual larval mortality rate equals the total number of eggs produced by an entire species population that year, minus the total mortality of mature individuals of that species. Periodic fluctuations in adult populations, by this line of reasoning, are due to a modification of one of the larval waste factors outlined above, or to some change in conditions which affect the early crab stages. In the case of the Xanthidae, these factors are the total amount of habitat available, food conditions, temperature conditions which may speed up or retard development and reproduction, population pressures, depredation, and competition for food. Thus, the reasoning used is based on a long-term basis in which fluctuating conditions and the resulting population change will balance out.

Current Transport

There are two main ocean currents which are responsible for water movement off the coast of California. These are the California Current, which transports water to the south, and the Davidson Current, which transports water to the north. The California Current prevails from February to October during the seasons of westerly winds and upwelling. In the fall when the westerly winds and upwelling cease, a counter current develops which, in November through

January, transports water as far north as the 48th parallel (Sverdrup, Johnson, and Fleming, 1942: 454, 502; and 726 for maps). In spite of some occasional nearshore reversal of currents, due to various meteorological conditions, the dominant flow of the California Current during the xanthid larval season is to the south. This would mean that any xanthid larva entering such a system during its five-week developmental period would be swept southward and metamorphose 50 to 100 miles from where it hatched. *Paraxanthias taylori* and *Cycloxanthops novemdentatus* at Monterey, California, would thus produce larvae settling at Point Conception, California, and those larvae from Point Conception would settle at Palos Verdes, California, and so on. Obviously this is not the case, for (1) there is no point of larval supply for Monterey, and (2) at 3- to 4-year intervals the distribution of these species would recede 50 miles or more southward. There must, then, be a current system or some other factor peculiar to the nearshore waters which maintains larvae spawned in a local area until they finish their cycle.

To see if such a factor exists, a series of simple float studies was employed in the first bay south of Resort Point, Palos Verdes Hills, California.

Experiment 1. Drift bottles were set out 3 hours before low tide and 3 hours after low tide on November 11, 1955. The bottles used were small, eighth-pint bottles, with colored markers inside. They were launched by means of a leather thong slingshot. Two observers plotted their drift pattern from the cliff top from 9:30 a.m. to 5:30 p.m. Though all of the markers remained in the bay, some of those placed closer to the point entered an eddy system in the mouth of the bay, while others moved towards the head of the bay and there entered a smaller eddy system, but none were washed to shore or out to sea.

Experiment 2. In May 1956, forty "drift arrows" were set out. The arrows consisted of 36-inch, weighted, wooden shafts with small cloth flags at the top. These were shot from the cliff into the bay with a hunting bow, and their drift recorded. These were not very satisfactory in that they were hard to see at distances greater than 200 yards. Most of the arrows in the bay were carried beyond Resort Point, and then southward, out of sight within 20 minutes. A few arrows came into the breaker zone and were washed ashore.

Experiment 3. On July 10, 1956, thirty drift cards were released at 6:00 a.m., one hour after low tide. In this case, the cards were placed just beyond the breaker zone and all floated out to sea and out of sight. Four of these cards were found that same afternoon by swimmers within a one-half mile radius of the bay. A fifth, and more significant card, was found 12 days later still adrift just off shore in the next bay south.

Experiment 4. On July 18, 1956, forty-five drift cards were set out at 10:00, 11:00, 12:00 and 1:00 o'clock but in each case were swept ashore, regardless of their launching point. On the first three attempts half of the cards were set in the middle of the bay and half at the mouth (by swimming out with them). Within 40 minutes after launching they were in the surf zone along the south side of the bay where they were gathered up. On the last attempt the writer placed the cards about 200 yards out beyond Resort Point opposite the mouth of the bay. These also drifted in towards shore where some were picked up by swimmers and returned.

Experiment 5. Thirty drift cards were set out in the bay at 12:00 noon, September 1, 1956. These drifted out of sight within 30 minutes after being released. Four of these cards drifted back into the bay late in the afternoon, and were picked up by swimmers. One more was found in the water within the bay, 8 days later. Another card was found on El Morro Beach 16 days later, and still one more was returned from Carlsbad Beach 19 days later.

Experiment 6. Thirty drift cards were released in the mouth of the bay at 1:40 p.m., September 1, 1956. These cards drifted into the beach and were collected there.

A great deal of additional work is needed before any conclusions can be reached as to the current patterns near Resort Point. The results obtained were of three types: (1) floats remained in a continuous eddy system; (2) floats left the bay but returned at a later time; and (3) floats drifted directly into the bay. It is interesting to note that a float was recovered in the water in the bay almost 2 weeks after being released. Others which had floated from the bay

returned and were picked up in the water. Still other cards were caught in an offshore current and carried far to the south.

It is evident that the currents around Palos Verdes are irregular and frequently shift direction within a short time. Wind, tide level, and bottom topography may all serve to create and alter these currents. It is also evident that the currents observed are peculiar to a narrow strip of water embracing the headland, and that the California Current has little or no effect here. That the California species of Xanthidae are not rapidly disappearing from Palos Verdes suggests this also. The writer believes that a portion of xanthid larvae are caught in a southerly current (Experiment 5) and die in the first crab stage when a suitable habitat is not found. This is suggested by first crabs and megalops clinging to drift algae, and by the deep water distribution of *L. h. diegensis*.

Macrocystis Beds

Along the major portion of the range of the California species of Xanthidae are found large beds of the giant brown kelp, *Macrocystis pyrifera*. This alga grows in water from 30 to 90 feet deep all along the rocky shores. In the summer it forms a very thick mat of growth at the surface which divides the outer oceanic water from a thin strip of water between the kelp beds and the shore. A single bed often extends for many miles along the coast without interruption.

Such dense, uninterrupted growths could serve to (1) protect larvae, (2) offer hiding places where the cycle could be completed, and (3) alter currents to maintain an inshore eddy system. Andrews (1945: 36) concludes that kelp beds at Monterey, California, check currents and wave action, and offer protection to developing larvae. Limbaugh (1955: 13) reports the "dumping" of long waves which reach the kelp beds, but states that short waves pass through them with little interference.

Of the animal life in the canopy of *Macrocystis* there are such forms as pelagic and nearshore fishes and invertebrates, especially larval forms (Limbaugh, 1955: 14). The writer's plankton net collecting did not indicate plankton to be more abundant in kelp beds, but the amount of work done is so small (18 net hauls, half in kelp beds), and accomplished under such awkward conditions (small skiff and inner-tube raft), that it is of no significance. Limbaugh records less plankton collected in the kelp beds than such places as over rocky nearshore bottom where plankton is abundant. He explains this by the abundance of fish which filter feed in the kelp beds and thus reduce the plankton there. However, difficulty in using a net in kelp beds may also explain this difference. The significant points demonstrated are (1) that schools of fish are attracted to feed in the kelp beds, denoting a concentration of plankton which probably seek shelter there, and (2) the presence of a large number of larvae inshore from the kelp beds. It seems apparent that the kelp beds and/or peculiar nearshore currents are holding the larvae and thus preventing a reduction of species along our coast.

Inshore Migration

Unless a mechanism such as that suggested above keeps the xanthid larvae close to their habitat area, the megalops stage must migrate inshore at the time of metamorphosis. The drift card Experiment 4 shows that currents are, at times, very favorable to inshore migration of the larvae. Rafting on drift algae may be a second method employed by xanthid crabs to migrate inshore. Cunningham (1898: 205), Lebour (1928: 499; 1947: 528–535), and Hiatt (1948: 204) report finding megalops and/or first crab stages along the beach. The writer has also recovered the megalops of *Pachygrapsus crassipes*, *Hemigrapsus nudus*, and *Lophopanopeus l. leucomanus* at the bay, thus suggesting that the megalops stage completes metamorphosis after reaching the adult habitat.

Early Crab Stages

The early crab stages of *Paraxanthias taylori*, *Lophopanopeus l. leucomanus*, and *Cycloxanthops novemdentatus* were found on many occasions along the Palos Verdes shore. These resemble the mature adults in carapace proportions and gross appearance. The young *Paraxanthias taylori* resembles the adult in color also while the young of *Cycloxanthops novemdentatus* and of *Lophopanopeus l. leucomanus* are of many different bright colors. These little animals are found in the smallest of cracks or

spaces between snail tubes, or even, in the case of *Lophopanopeus l. leucomanus,* in the dense coralline turf on top of rocks in the xanthid habitat. Edcysis is probably carried out in the security of such places. The early crab stages molt every 10 to 15 days and grow rapidly in their first year. The smallest crab stages feed on microscopic red algae which grow in the shaded areas of their habitat. The small crabs are easily attracted to raw meat, such as abalone, but it is doubtful if their diet contains much of this. The megalops and first crab stages have many enemies in blennioid fishes and other crabs. While making periodic underwater observations, it was noted that blennioid fish occupy the xanthid habitat at high tide. These fish spend much of their time lying in wait on top of algal covered rocks. At times they were seen to dart away from their hiding place to catch isopods. When small xanthid crabs were dropped nearby the fish made a serious effort to capture them. This suggests that the blennioid fish may be preying upon the xanthid crabs. To test this suggestion, stomach examinations were made on 51 blennioid fishes of the following species: 31 *Clinocottus analis* (Girard), 5 *Oligocottus maculosus* (Girard), 3 *Artedius lateralis* (Girard), 5 *Gibbonsia eligans* (Cooper), and 7 *Gibbonsia metzi* Hubbs. The stomachs contained many limpets, snails, polychaetes, crustaceans, and small fishes. Of the Crustacea there were isopods, amphipods, *Caprelia,* stomatopods, shrimp, porcellanids, hermit crabs, and the following Brachyura: *Pachygrapsus crassipes, Lophopanopeus* spp., *Pugettia producta,* and *Herbstia* sp. In the stomach contents crustaceans were dominant, while mollusks were second in volume. Both adults and megalops of the genus *Lophopanopeus* were found, thus establishing the blennioid fish as enemies of the Xanthidae.

SUMMARY

1. Sexual dimorphism of the California Xanthidae is manifested in the abdomen of mature and submature specimens.

2. The immature, submature, and mature specimens of *Cycloxanthops novemdentatus, Lophopanopeus l. leucomanus, L. bellus diegensis,* and *Paraxanthias taylori* may be separated by noting the width of the abdominal segments, the length of the lateral abdominal hair, the presence or absence of the abdominal lock, and the condition of the pleopods.

3. The internal and external genitalia are similar in all species of the California Xanthidae and are described for both sexes.

4. Xanthid crabs breed in a hard shell condition. The male is always above the female transferring sperm to her vulvae by means of the intromittent organs.

5. *Lophopanopeus* spp. begin breeding earlier in the season and have more broods per season than the other genera. *Cycloxanthops novemdentatus* has the shortest breeding season.

6. Eggs vary in number, with the species and with the size of the individual, from 1,000 to 45,000. They are attached to the pleopods and there aerated and cleaned by the female until hatching.

7. Hatching occurs generally at night. There is no molt between the prezoeal and first zoeal stages. There are four zoeal and a single megalops stage in the xanthid life cycle (which requires about five weeks to complete).

8. The xanthid zoeae are photopositive and swim by means of the maxillipeds or with maxillipeds and telson. The megalops use their pleopods for locomotion.

9. Zooplankton probably constitutes the larval food in nature. Zoeal feeding methods are described herein.

10. The process of molting of the zoeae and megalops is essentially the same as in the adult.

11. Data collected suggest that peculiar eddy currents exist in bays and coves along the California coast which hold the developing larvae close to shore and prevents their removal by the southerly California Current.

12. *Macrocystis* beds help isolate developing larvae, offer wave protection and perhaps hiding places as well.

13. Megalops of the Xanthidae probably metamorphose in the adult habitat since the first crab stages were found there in abundance.

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Land Crabs and Fission Products at Eniwetok Atoll[1]

EDWARD E. HELD[2]

PERIODIC STUDIES of the effects of the atomic testing program on the biota of the Marshall Islands have been made since 1946 by the staff of the Applied Fisheries Laboratory, University of Washington (Biddulph and Cory, 1953; Donaldson *et al.*, 1948, 1949, 1956; Palumbo, 1955; Seymour *et al.*, 1957; AEC reports UWFL-7, -16, -19, -23, -33, -42, -43). During the testing program at Eniwetok in 1954 a continuous biological survey was initiated. In this report the portion of the survey concerned with the uptake of radionuclides by the land hermit crab, *Coenobita perlatus* Edw. T.,[3] is presented. Results of possible ecological and physiological significance in the movement of strontium and cesium through the food cycle have been obtained. Strontium-90 concentration in the land crab skeleton may be a sensitive index of biologically available radiostrontium in the environment.

Coenobita is an omnivorous scavenger which feeds primarily on land plants and on detritus washed up on the beaches. It is primarily nocturnal and spends the daylight hours hidden in shrubs or under debris.

The crabs were taken from Belle Island (Bogombogo) which lies 2.3 nautical miles southwest of the site of the Mike test of 1952 and the Nectar test of 1954. This island is downwind from the site of these tests.

Prior to the Mike test Belle Island had a covering of shrubs, coconut palms, and trees (Palumbo, MS). The island was denuded by the blast in November 1952, but by April 1954 it had regained a heavy growth of shrubs, principally *Scaevola frutescens* and *Messerschmidia argentea*. The regrowth was from seedlings and stumps of old plants. A rookery of fairy and noddy terns had also become established. Belle Island was again denuded by the Nectar test of May 1954 save for stumps and some stripped branches. Dead birds and fish were found in the center of the island as well as along the shores. One dead *Coenobita* was found, but almost all of a population of about 50 in one pile of debris survived, probably because of the protection of the debris and their habit of quickly withdrawing into their shell when disturbed. It is probable that they withdrew at the first flash of light before the blast reached them.

Belle Island regained a lush cover of shrubs by August of 1954, less than three months after the Nectar test, and a fairy tern egg found three months later, in late November, marked the beginning of a new rookery on the island.

ACKNOWLEDGMENTS

The wholehearted cooperation of all members of the staff of the Applied Fisheries Laboratory, who at various times participated in the collection and preparation of samples, made this report possible. Miss Dorothy J. South supplied the results of the radiocesium, radiocerium, and some radiostrontium determinations. The cooperation of the U. S. Atomic Energy Commission Division of Biology and Medicine and the Eniwetok Field Office, Task Group 7.1, and Holmes and Narver greatly facilitated the field collecting.

METHODS

Collections were made at approximately daily intervals commencing with the third day following Nectar until the ninth day. Thereafter, the interval between collections was progressively lengthened to approximately monthly intervals. Three crabs were taken at each collection except that in three instances five, and in one instance, only two were taken.

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[3] We are grateful to Dr. C. H. Edmondson, Bernice P. Bishop Museum, Honolulu, Hawaii, for identification of the species.

Samples of carapace (exoskeleton), muscle, hepatopancreas ("liver"), gut with its content, and gill were removed, either from the fresh or frozen specimens, at the Eniwetok Marine Biological Laboratory. The tissues were weighed at the time of dissection and then dried. The packaged dried samples, together with data cards, were sent by air mail to the Applied Fisheries Laboratory, University of Washington, for further processing.

The dried samples were ashed at temperatures up to 550° C. on stainless steel counting plates and were counted in an internal gas-flow counting chamber. The beta counts per plate were converted to total disintegrations per minute per gram (d/m/g) of wet tissue, as of the date of collection, by correcting for sample weight, geometry, backscatter, self-absorption, coincidence, and decay. (See WT-616 (UWFL-33) for a more complete discussion of these procedures.)

The decay corrections for all tissues except carapace were based on the decay rate of a soil sample collected at Belle Island the day after the Nectar shot. (This decay rate was determined by beta counting.) Decay corrections for the carapace were based on the decay rate of $Sr^{90} + Y^{90}$ and Sr^{89}, which constituted virtually 100 per cent of its activity at the time the chemical determinations were made. The decay correction factors ranged from 1.09 to 12.7.

The variation in amount of radioactivity for each tissue at each collection date, although great, was not great enough to obscure general trends in changes of radioactivity with time or differences in levels of radioactivity between tissues.

The term "activity" as used here means radioactivity per unit weight.

"Rate of decline" refers to the rate at which radioactivity is decreasing in a given tissue, organ, or organism in its native environment.

Levels of activity in the crab tissues three days after the Nectar test ranged from 5×10^6 d/m/g in the gut to 7×10^4 d/m/g in the muscle (Figs. 1, 2). The rate of decline of activity decreased with time and was different for each tissue, but in general followed the same trend as the decay of mixed fission products during the first 200 days. Thereafter the rate of decline for each of the crab tissues approached a constant value with a half life in excess of 20 years.

This half life is dependent on factors which include relative abundance and availability of radionuclides in the food and/or environment, rate of decay of radionuclides absorbed, biological half life, and selective uptake of radionuclides. Each of these, except the rate of physical decay, is in turn dependent on varying environmental and physiological conditions. The terms "ecological half life of radioactivity," or more briefly, "ecological half life" and "rate of decline" will be used to include these factors. Ecological half life will be used as the time required for an organism, or its tissues or organs, in its native environment to lose 50 per cent of its radioactivity. When the ecological half life and physical half life are equivalent (rate of decline = rate of decay), the tissue in question must be at equilibrium with respect to the radioisotopes it contains. For single isotopes an ecological half life greater than the physical half life (rate of decline < rate of decay) indicates accumulation of the isotope. In the converse situation where the ecological half life is less than the physical half life, a net loss of the isotope is indicated. This condition could result from loss of the isotope by the environment, or eco-system, or from a physiological change in the organism or its primary food source. Such physiological changes may be transitory or seasonal.

The increase in radioactivity over preshot levels during the first few days after the Nectar test was less in muscle and carapace than in the three other tissues by a factor of 5 to 10. Maximum post-Nectar levels of activity were 100 to 250 times greater than pre-Nectar levels in gut, liver, and gill, but only 22 and 26 times greater in muscle and carapace respectively. The lower rate of accumulation in muscle and carapace would be expected since the material must be absorbed from the gut and hepatopancreas where some selection takes place. The specific patterns of changing radioactive content of the tissues with time, the rate of decline, will be presented individually for each tissue.

The amounts of radioisotopes involved are so

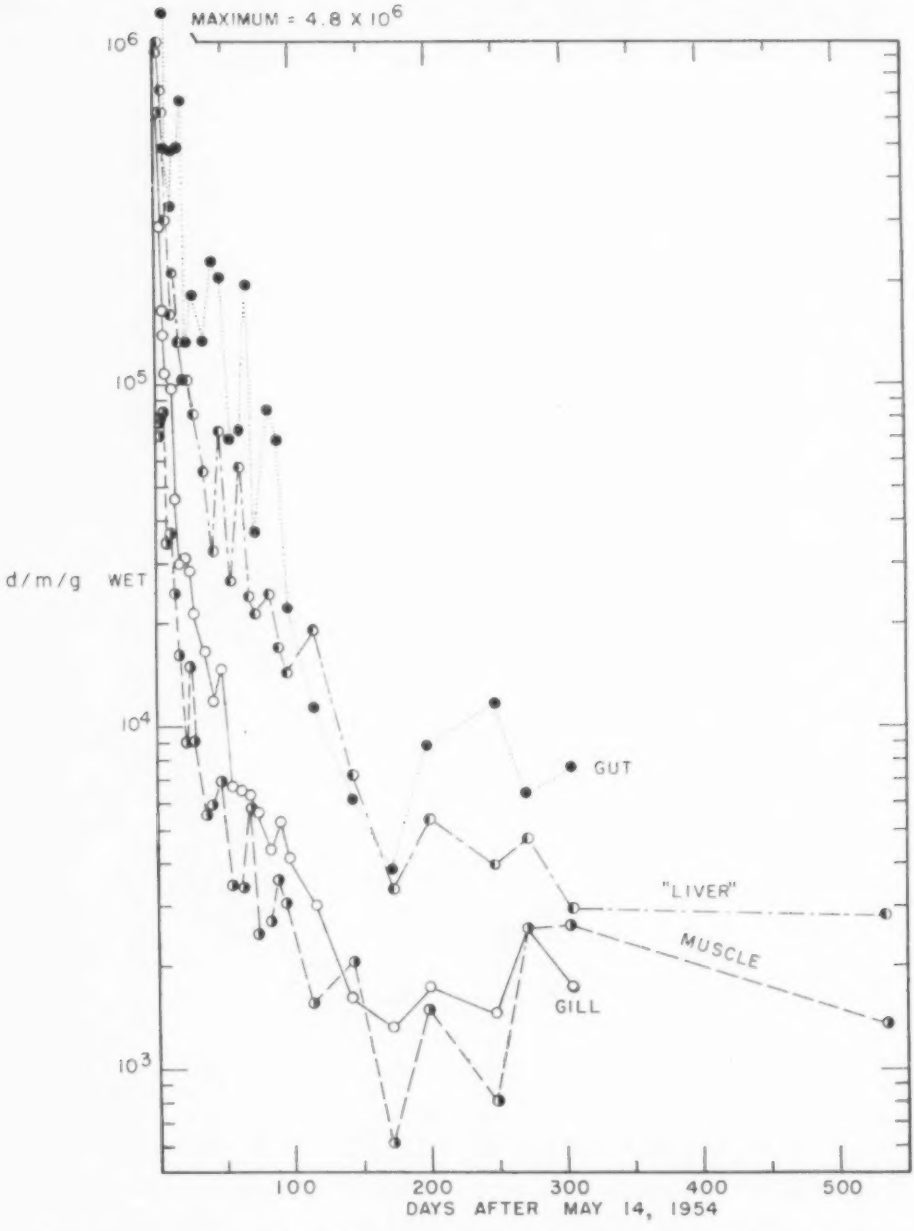

FIG. 1. Beta-activity in *Coenobita* gill, muscle, hepatopancreas ("liver"), and gut on successive collection dates. Values in disintegrations per minute per gram wet weight.

small that they probably do not constitute a significant proportion of the naturally occurring isotopes. If, for example, a tissue contained 10^7 d/m/g wet of Sr^{90}, or 5,000 times the maximum level found in the hermit crab, this would represent only 0.02 mg. of strontium, or about 10^{-5} per cent of the ash weight. The presence of strontium has been reported qualitatively in crustacea and a quantitative estimate of about 1 per cent strontium has been given for the ash of *Eupagurus bernhardus* (Vinogradov, 1953).

RESULTS

Exoskeleton

The carapace was taken as the sample of exoskeleton. It is easily removed, separated from other tissues, and washed free of possible external contamination.

The radioactivity in the carapace due to long-lived isotopes remained approximately constant throughout the period of 537 days during which collections were made. This was determined by recounting all of the samples approximately 600 days after the Nectar test (Figs. 2, 3).

Radiochemical analysis of 18 samples taken at various times during the collecting period (Table 1), and three samples taken 35 days before Nectar, demonstrated that virtually all of the long-lived activity was 28-year Sr^{90} and its Y^{90} daughter.[4]

The nearly constant level in the carapace (ecological half life $\cong$ physical decay) indicates that this tissue quickly reaches and maintains equilibrium with the available strontium. Gross, Taylor, and Watson (1954) report a plateau of retention of Sr^{90} in rats during continuous feeding at the same rate, and apparent shifting of the plateau with change in daily dose.

It would be expected that this relationship also applies to available calcium, which is metabolically similar to strontium, and to 54-day Sr^{89}, and possibly to Ba^{140}, which at the time the radiochemical analyses were made was present in amounts too small (< 0.2 per cent of total activity, according to Hunter and Ballou, 1951) to be determined by the method used.

[4] Results of calcium analyses of 74 samples of carapace made since submission of the MS give a mean of 158±30 mg. Ca/g wet, and 15,000±4900 strontium units.

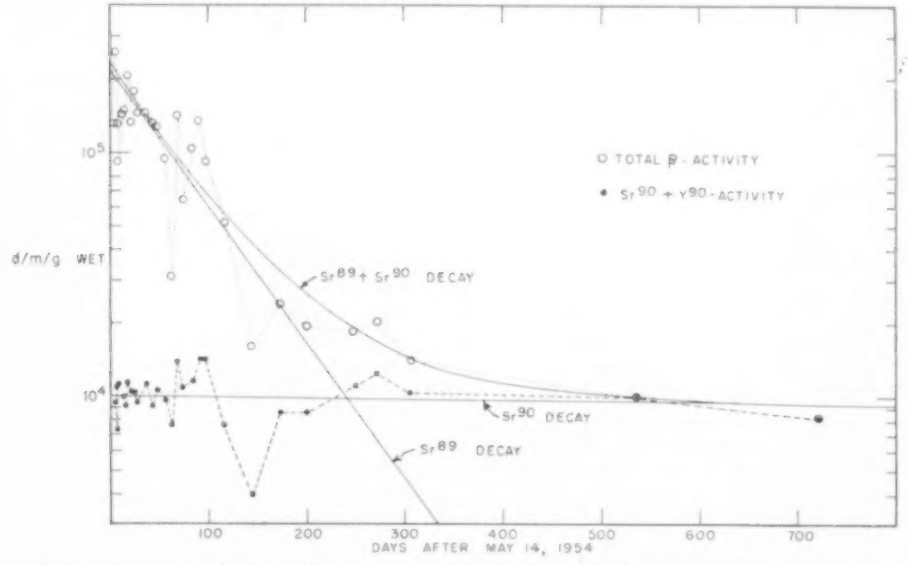

FIG. 2. Radioactivity in *Coenobita* carapace on successive collection dates compared with the decay of radiostrontium. Values in disintegrations per minute per gram wet weight.

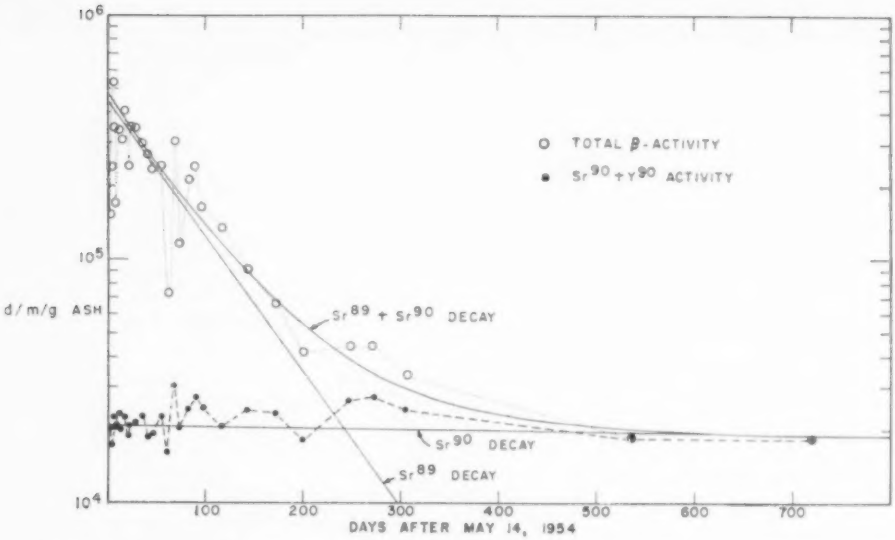

FIG. 3. Radioactivity in *Coenobita* carapace on successive collection dates compared with the decay of radiostrontium. Values in disintegrations per minute per gram of ash.

The amount of Sr^{89} present in the carapace immediately after Nectar was calculated from the yields given by Sullivan (1949) on the basis of the average amount of Sr^{90} in the 44 specimens collected during the first 50 days following Nectar, less the amount present before Nectar. The relative radioactivity of the two isotopes was calculated from their specific activities. A theoretical decay curve was then calculated for the combined Sr^{89}, Sr^{90} + Y^{90} contributed by the Nectar test and the Sr^{90} + Y^{90} residual from prior tests. Figures 4 and 5 show the actual values superimposed on this theoretical curve. Although there were no specific radiochemical determinations early in the period following Nectar, it is reasonable to assume that the exoskeleton has a high degree of selectivity for strontium and that equilibrium must be reached within a few days at most. The assumptions are further supported by decay curves which approach the theoretical curve (Fig. 4).

The relatively low levels of activity at 145 days post-Nectar are a reflection of a change in ratio of ash weight to wet weight; Figure 4 represents the data on an ash weight basis. The change in ratio may be associated with molting, but observations were not made at frequent enough intervals to confirm or deny such an association.

Contributions of radiostrontium to the crab skeleton at Belle Island from past tests at Eniwetok and Bikini are represented in Figure 5. The pre-Mike level is an approximation since it is based on a single specimen and there was, unfortunately, no biological survey during the 1950 tests. The pre-Nectar curves were derived by the method outlined above. The Mike test contributed about twice as much activity as the Nectar test; fallout from the pre-Mike tests and the Bikini tests of 1954 together contributed about 5 per cent of the total Sr^{90} activity.

Sr^{90} on the island is being maintained at an essentially constant level (decreasing only with physical decay), if the omnivorous hermit crab can be considered an accurate index of biologically available strontium. However, the ratio of the strontium in the crab skeleton to that in food items is not known. Judging from the meager data presently available, the radiostrontium content of the crab skeleton is more than

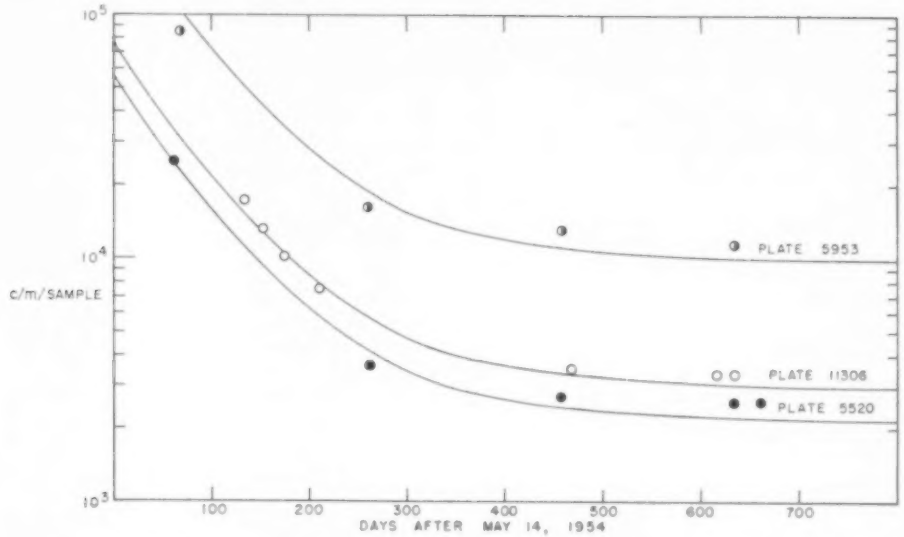

FIG. 4. Decay of beta-activity in three *Coenobita* carapace samples, each compared with the theoretical decay curve (solid lines) for $Sr^{89} + Sr^{90}$ from Figures 2 and 3.

ten times that in land plants on a wet weight basis and is more than three times that in soil on a dry weight basis.

Muscle

Isotopes with half lives greater than 20 years contributed nearly all of the activity in muscle tissue 35 days before the Nectar test. Cs^{137}, $Sr^{90} + Y^{90}$, and $Ce^{144} + Pr^{144}$ accounted for 84, 10, and 1 per cent respectively, of the total activity in muscle tissue collected in February and November, 1955, and analyzed in January and March, 1956. Similar levels, 67, 10, and 1 per cent, were found in coconut crab muscle from Rongelap Atoll (UWFL-43, table 14). In contrast to the exoskeleton, muscle tissue had a variable, though generally decreasing, level of long-lived isotopes throughout the post-Nectar collecting period (Fig. 6). Between 150 and 200 days post-Nectar, the total activity in muscle was due primarily to the long-lived isotopes, as evidenced by the increased ecological half life. The level of total activity in muscle at 172 days (after Nectar) is one-sixth the pretest level, while the level of long-lived isotopes at that time is one-eighth that of the pretest level; subsequently there is an increase in activity. Since both the total activity and the long-lived activity increased by approximately equivalent amounts, the increase must be due to an increased net rate of uptake, reflecting a change in the physiology of the crab or a change in the

TABLE 1

TOTAL β-ACTIVITY AND $Sr^{90} + Y^{90}$ IN *Coenobita* CARAPACE

(Determinations made in January and February, 1956. Averages of three samples and their standard errors are given.)

DATE COLLECTED	TOTAL β-ACTIVITY JAN.–FEB., 1956 D/M/G WET	$Sr^{90} + Y^{90}$ ACTIVITY FEB., 1956 D/M/G WET
4/15/54	6900 ± 672	7454 ± 952
5/26/54	10243 ± 968	9763 ± 975
8/12/54 or 8/19/54	14851 ± 1413	15568 ± 1237
10/5/54	4362 ± 431	4043 ± 385
3/15/55	10368 ± 581	11281 ± 479
2/9/55	12516 ± 1594	12532 ± 1484*

* Average of duplicate aliquots of three pooled samples as determined by Dorothy J. South, Applied Fisheries Laboratory.

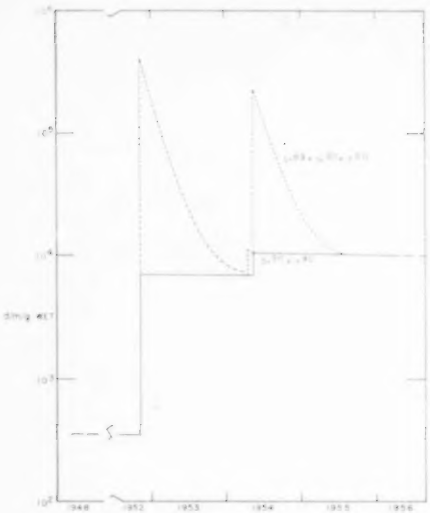

FIG. 5. Radiostrontium in *Coenobita* skeletons at Belle Island.

conditions in the environment, leading in this case to a greater availability of Cs^{137} to the crab. The latter possibility is the more easily explained by the observations.

The same pattern of decrease in activity followed by a rise is evident in the gut and liver of the crab, the leaves of the shrubs, *Scaevola* and *Messerschmidia*, and the muscle of the field rat, *Rattus exulans*, from Janet Island (Engebi) which is also in the northern part of Eniwetok Atoll (Lowman, MS). During the first 200 days (May–November, 1954) rainfall at Eniwetok averaged about 4 inches per month, while for the following 150 days (December–April) the average monthly rainfall was about 0.3 inches (Fig. 7). Since individual variation in the level of activity is great there would be little reason to accept the validity of the correlation were it not repeated in the plants and in rat muscle, which are also high in Cs^{137} content (56 per cent of the total activity in the latter). It appears likely, therefore, that the changes in activity in the crab and rat muscle reflect some underlying mechanism associated with rainfall which is responsible for changes in the levels of activity in the plants.

There could be one or several factors involved in the association with rainfall including, for example, such things as exchangeability of cesium, total amount of root surface available during the wet as compared with the dry season, and increasing acidity of the soil on drying (Stone, 1951). More complete series of radiochemical determinations of the radioisotopes in both plants and soils are needed to understand the mechanisms involved. Contrary to results reported on relative availability of cesium and strontium to plants in other soils, cesium appears to be more readily available than strontium in the atoll island soil (Selders *et al.*, 1955; Neel *et al.*, 1953; Larson *et al.*, 1953; Nishita *et al.*, 1954; Ophel, 1955).

The short half-life isotopes that contributed to the activity in the muscle during the first 150 days are not known. The rate of decline during this period was approximately the same as the rate of decay for mixed fission products.

Radiocesium content of hermit crab muscle is about 1.5 times that in plants (1,000 d/m/g : 700 d/m/g) on a wet weight basis. The radiocerium levels in the soil were too low (< 1 per cent of the total activity) to be detected by the radiochemical methods used.

Hepatopancreas ("Liver")

The rate of decline of activity of the hepatopancreas or "liver" of the crab during the first 175 days post-Nectar is not significantly different from the rate of decay of mixed fission products. This is true despite the fact that there was a pre-existing level of long-lived activity approximately equal to the level existing 537 days post-Nectar. Sr^{90}, Cs^{137}, and Ce^{144} were found.

Equilibrium must be quickly reached and maintained at a constant level proportional to the availability of the long-lived isotopes. Levels of activity were 8,500 d/m/g pre-Nectar, reached a maximum of 10^6 d/m/g four days post-Nectar, and declined to a level of 3,000 d/m/g at 305 days and 537 days (Fig. 1).

Gut with Content

The hermit crab gut with its content was generally more variable than the liver in levels of activity, especially during the first month post-Nectar. This difference is to be expected, since ingested food would have variable amounts of

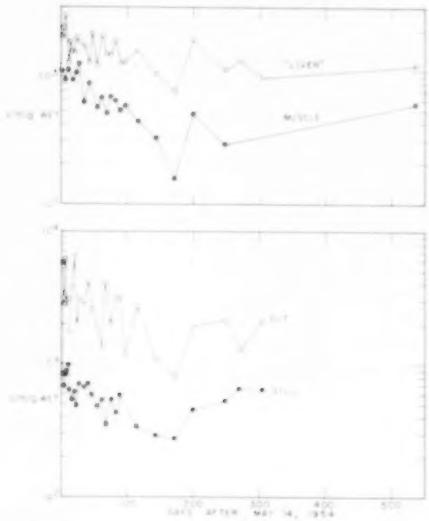

FIG. 6. Counts per minute per gram in *Coenobita* tissues as of 600 days after May 14, 1954, plotted for each collection date.

surface contamination and not all crabs would feed on the same thing at any one time.

Initially, following the Nectar test, the gut had the highest level of activity of all tissues (5×10^6 d/m/g). The activity in the gut also had the shortest ecological half life of all tissues during the first 100 days post-Nectar. By 100 days, the levels of activity in gut and liver approached each other and their ecological half lives were about the same, although the gut remains so variable from collection to collection that only an approximation can be made. The activity in the carapace by 100 days was higher than that in the gut even though the latter had the highest initial activity. This variation is, of course, due to the different rates of decline, which reflect selection of the long-lived isotope Sr^{90} by the carapace.

No chemical analyses of gut samples were made.

Gill

The rate of decline of activity of the gill of the crab is more rapid than the rate of decay of mixed fission products during the first 10 to 20 days post-Nectar, but thereafter approximates the same rate until the 200th day. The early high levels may be due to contamination of the surface of the gills and possibly to excretion of salts through the gills. From the tenth day on, the pattern of decline of the gill is the same as that of muscle. The activity level was generally higher in the gill than in the muscle by less than a factor of two on a wet weight basis.

No chemical analyses of gill tissue were made.

DISCUSSION

During the first 150 days following a nuclear detonation the rate of decline of radioactivity in organisms on atoll islands may be considered to approximate the rate of decay of mixed fission products. This conclusion is supported by data from collections at Rongelap Atoll in 1954 (AEC reports UWFL-42, -43). Errors in the estimate of future levels based on this approximation would tend toward the prediction of higher levels than would actually be attained in the first 150 days. The wide spectrum of available radionuclides present in the early period following a detonation may be available to individual organisms in extremely minute amounts; consequently, differences in the rate of decline reflecting selectivity by an organism are masked, since various combinations of the short-lived nuclides could result in an approximation of mixed fission products decay. The availability of a wide spectrum of radionuclides during the first few days might be due not only to the presence of these nuclides, but also to the fact that they could potentially be absorbed directly by the leaves of plants and thus circumvent fixa-

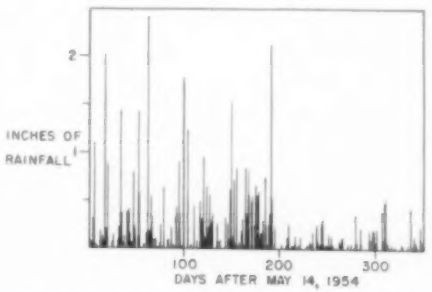

FIG. 7. Rainfall at Eniwetok Island (from records of Detachment 2, 57th Strategic Reconnaissance Squadron, Medium, Weather, USAF).

tion on the soil. Residual contamination from fallout a year or more old would have an insignificant effect on rate of decline during the first 150 days if the total contamination from each detonation were of the same order of magnitude or the first less than the second. This was the case following the Nectar test at Belle Island, which had residual contamination from the Mike test (1.5 years previous to Nectar).

After approximately 150 days following fallout, the rate of decline becomes less than the rate of decay of mixed fission products, reflecting the relative concentration by the island organisms of the long-lived isotopes Cs^{137} and Sr^{90}. Other isotopes, both fission products and neutron induced products, are involved, but Cs^{137} and Sr^{90} with their daughters account for 80 per cent or more of the total activity in land organisms two years following the Nectar test. This is true even though these isotopes together contribute only 18 per cent of the total activity from mixed fission products at that time. On a basis of fission yields, Cs^{137} and Sr^{90} would contribute no more than 35 per cent of the total activity even if all of the activity at Belle Island were from the Mike test. Ce^{144} activity is low (1 per cent in crabs) in the island organisms because of its low rate of uptake by land plants from soil (Neel, 1953). On the other hand, in marine organisms radiocerium does enter into the food chain in significant amounts, 26–71 per cent of the total β-activity, according to AEC report UWFL-43, Bonham, MS.

It appears, therefore, that in so far as the long-lived radioactive fission products strontium, cesium, and cerium are concerned there is what might be called a strontium–cesium food cycle on land and a cerium food cycle in the lagoon.

SUMMARY

1. Periodic determinations of radioactivity in land crabs from Belle Island, Eniwetok Atoll, were made over a period of nearly two years following the 1954 atomic testing program.

2. Radioactivity in the exoskeleton was found to be due almost entirely to radiostrontium and the Y^{90} daughter of Sr^{90} and remained at a nearly constant level, excepting physical decay.

3. An estimate of contributions of radiostrontium from previous tests to a crab skeleton at Belle Island is given.

4. Long-lived fission products in muscle tissue consisted of 84 per cent Cs^{137}, 10 per cent $Sr^{90} + Y^{90}$, and 1 per cent $Ce^{144} + Pr^{141}$.

5. A possible association between the availability of cesium and rainfall is suggested.

6. During the first 150 days following a nuclear detonation the rate of decline of radioactivity in organisms on an atoll island may be considered to approximate the rate of decay of mixed fission products.

7. In so far as the long-lived fission products strontium, cesium, and cerium are concerned there appears to be a strontium–cesium food cycle on land and a cerium food cycle in the lagoon.

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A New Hawaiian Percoid Fish, *Suttonia lineata*, with a Discussion of Its Relationships and a Definition of the Family Grammistidae[1]

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THE IMMEDIATE RELATIONSHIPS of the fish described here appear clear cut. However, the systematic position of the "pseudogrammid" group of genera to which it belongs is a matter of considerable controversy; the greater part of the present paper will be devoted to this subject.

The "pseudogrammid" genera (Table 1) are made up of a small number of serranid-like fishes which for the moment may be sufficiently defined as having a single enlarged (though frequently concealed) spine at the upper end of the preopercular border (Fig. 2*a*), and an incomplete or interrupted lateral line. Four genera are included in the group; they may be distinguished as follows:

1 Preopercular spine directed downward (this character not recorded for *Rhegma gregoryi* or *Pseudogramma guineensis*) 2
Preopercular spine directed somewhat upward. No large lateral line pores between the eyes; in the adult *Aporops bilinearis* there is a frilled collar behind the tube of the anterior nostril, and just ahead of the preopercular spine is a small patch of glandular tissue that may bear black, hairlike processes ..... **Aporops**

2(1) No tentacle over the eye 3
A single, fleshy tentacle over each eye ..... **Rhegma**

3(2) Preopercular spine broad-based and triangular (Fig. 2*a*) ..... **Pseudogramma**
Preopercular spine elongate and downwardly curved (Fig. 1) ..... **Suttonia**

Aporops appears to be rather distinct from the other three genera. Whether *Rhegma* and *Suttonia* should be considered as more than subgenera of *Pseudogramma* is open to question.

Genus SUTTONIA Smith, 1953

TYPE SPECIES: *Suttonia suttoni* Smith, 1953 (East Africa). The only other species attributed to the genus is the one described below.

Suttonia was differentiated by Smith (1953: 549) from *Pseudogramma* and *Aporops* as follows: "Scales all cycloid. Preopercular spine large, sabre shaped and trough like. Nasal tube longer than interorbital width. Interorbital mostly naked. Palatines subparallel. A single lateral line." Aside from the fact that in the Hawaiian specimens the palatines are not particularly subparallel, there seems to be little to add or subtract from Smith's diagnosis.

Suttonia lineata new species
Fig. 1 and Table 1

HOLOTYPE: USNM 177950, 78 mm. in standard length, collected with a commercial fish poison off the Waianae coast of Oahu, Feb. 3, 1958, by Gosline, Takata, *et al.* in 10–12 fathoms of water.

PARATYPES: UH 2460, 5 specs., 36–72 mm., with the same data as the holotype.

There are VI dorsal spines in the holotype, VII in all five paratypes. In the larger specimens

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TABLE 1

CERTAIN COUNTS IN "PSEUDOGRAMMIDS"

SPECIES	SOURCE	DORSAL	ANAL	PECTORAL	SCALES	GILL RAKERS[1]
Aporops						
bilinearis	Schultz, 1953	VII, 23–24	III, 19–21	16–18	ca 59–71	16–18
alfreei	Smith, 1953	VI–VII, 23–24	III, 21	15	80	×
japonicus	Kamohara, 1957	VII, 21	III, 16	×	ca 60	13
Rhegma						
thaumasium	Kanazawa, 1952	VII–VIII, 20–24	III, 16–19	16–18	47–52	14–17
gregoryi	Breder, 1927	VII, 15	III, 12	×	48	×
bermudensis	Kanazawa, 1952	VII–VIII, 19	III, 16	14	40–42	15
Pseudogramma						
polyacantha	Schultz, 1953	VII–VIII, 15–18	III, 15–18	17–18	ca 50–54	17–18
guineensis	Norman, 1935	VII, 20	III, 16–17	×	48?	×
brederi	Longley and Hildebrand, 1940	VII, 21	III, 17	14	50	×
Suttonia						
suttoni	Smith, 1953	VII, 23–24	III, 19	16	60	15
lineata						
Holotype		VI, –	III, –	16	64	—
Paratypes		VII, 23–24	III, 20–22	16	58–61	16

[1] Including rudiments.

the soft dorsal and anal rays are not only covered with skin and scales, but the basal portion of the rays becomes embedded in a heavy layer of fatty tissue. As a result the counts for these fins are based on only three paratypes, one in which the fins have been dissected (given first), and the two smallest: soft dorsal rays, 23, 23, 24; soft anal rays, 20, 21, 22. In the paratype dissected for the fin counts there are 5 gill raker rudiments above, 1 at the angle, and 10 rakers and rudiments below. Other counts are given in Table 1.

There seems no reason to give a long description of *Suttonia lineata*, for most of Smith's (1953) account of *S. suttoni* applies equally well to *S. lineata*. In one paratype there are two short, muscular caeca on either side of the pyloric end of the stomach. The pore configuration of the head is that of *Pseudogramma* rather than *Aporops*, i.e., there are two slitlike pores in the interorbital. There is also an especially large pore, larger than in either *Pseudogramma* or *Aporops*, at the very base of the free preopercular border. The preopercular spine is elongate, downwardly curved, and has a deep, sharply demarcated, central gutter filled with glandular tissue. There are no externally visible spines on the operculum, and the opercle itself has almost exactly the shape of that in *Pseudogramma* (Fig. 5). The teeth are about as described in *Suttonia suttoni* and almost exactly duplicate the dentition of *Pseudogramma polyacantha*. The nasal organ is also like that of *Pseudogramma* (Fig. 2*b*). As Smith (1953) has already noted, the scales on the top of the head stop short of the interorbital and the interorbital pores in *Suttonia;* in *Pseudogramma* the squamation extends forward nearly to the front borders of the eyes and surrounds the interorbital pores.

The most obvious differences between *Suttonia suttoni* and *S. lineata* lie in coloration. A color description of the latter species made after the specimens had been a week in formaldehyde is as follows: "Body reddish gray; dorsal, anal and caudal with a narrow white border. Lower half of head (below a rather abrupt transition zone running through the lower border of eye), pectorals and pelvics reddish. Upper half of head darker, except for a prominent light red middorsal band running from the dorsal origin to the tip of snout, this band most prominent forward." When first taken, the specimens had an

FIG. 1. *Suttonia lineata*. Paratype, 72 mm. in standard length.

essentially similar coloration. In alcohol, the smallest of the paratypes show a certain amount of reticulation on the lower portion of the head. Unlike *S. suttoni*, *S. lineata* has no dark opercular spot and no lines along the sides.

Aside from the characters noted in the last sentence, *S. lineata* seems to differ from the description and figure of *S. suttoni* given by Smith (1953) principally in the lack of externally visible opercular spines. The two forms are obviously close; they seem to differ to about the same degree as most Hawaiian and East African counterparts do.

Lineata (L.): lined, for the prominent middorsal stripe on the head.

"PSEUDOGRAMMID" RELATIONSHIPS

Though there is little doubt about the close interrelationship of the genera assigned to the "pseudogrammid" group—*Aporops, Rhegma, Pseudogramma,* and *Suttonia*—there is considerable disagreement about the family to which these genera should be assigned (see Table 2). Regan and Norman have included them in the Serranidae; Schultz placed them in the Pseudochromidae; and Smith erected a separate family for them.

FIG. 2. *Pseudogramma polyacanthus*. *a*, Lateral view of head; *b*, diagram of right nasal organ, with covering tissues removed but with the position of the nostrils indicated for orientation.

In an attempt to resolve the problem of "pseudogrammid" relationships, partial or complete skeletons have been prepared of the typical serranid *Epinephelus quernus* (from Hawaii), of *Pseudogramma polyacanthus* (from Hawaii), *Plesiops corallicola* (from the Marshalls; see Inger, 1955: 266), and *Pseudochromis tapeinosoma* (from the Gilberts). Certain aspects of the soft anatomy of these species and of *Epinephelus hexagonatus* (from the Phoenix Islands), *Aporops bilinearis* (from Tahiti), *Suttonia lineata* (paratypes), and of *Grammistes sexlineatus* (from the Line Islands) have been examined. When generic names are used alone in this paper, they refer to the above species.

Soft Anatomy. The only internal soft structure that has hitherto been used in the classification of the "pseudogrammid" fishes is the presence of two heavy-walled pyloric caeca (Smith, 1953: 548, fig. 2). In *Epinephelus* pyloric caeca are relatively numerous (cf. Suyehiro, 1942: 161, fig. 112), and in *Plesiops* and *Pseudochromis* they are completely lacking.

A second feature that seems at least equally significant is the structure of the nasal rosette. In *Epinephelus, Pseudochromis,* and *Plesiops* (Fig. 3*a*) the rosette is small. In *Pseudogramma* (Fig. 2*b*) the nasal epithelium is extended both upward below the nasal bone and downward below the lacrimal.

In view of this difference between nasal organs, the brains in specimens of *Epinephelus* and *Pseudogramma* were uncovered dorsally. However, no conspicuous differences were seen.

Attempts to investigate the nature of the air bladder were unsuccessful.

In *Aporops, Pseudogramma,* and *Suttonia* there is an area of presumably glandular tissue just ahead of the preopercular spine. In *Aporops* this area may be discerned externally, but in the other two genera it is concealed by the skin and scales.

Cranium. The crania of *Epinephelus, Pseudogramma* (Fig. 4), *Plesiops,* and *Pseudochromis* differ very little from one another. In *Epinephelus* there is no conspicuous otic bulla as there is in the other three, and the supraoccipital has a well-marked crest. *Pseudogramma* has a median opening to the sensory canal system between the frontals (Fig. 4*a*), but this is

lacking from the closely related *Aporops* as well as from the other three genera.

Nasal and Circumorbital Bones. In *Epinephelus, Plesiops* (Fig. 3*a*), and *Pseudochromis* the nasal bone is merely a weakly S-shaped tube bearing the front of the supraorbital lateral line. In *Pseudogramma* (Fig. 3*b*) the S-shaped tube is present but bears a flange that extends laterally over the upper end of the enlarged nasal organ.

In *Epinephelus* the first circumorbital (preorbital) is considerably expanded dorsoventrally; its upper surface articulates with the bottom edge of the lateral wing of the prefrontal, and its posterior edge is suturally joined to the small second element of the circumorbital series. It is the relatively narrow (dorsoventrally) third element that provides the subocular shelf. In *Pseudogramma* (Fig. 3*b*), *Plesiops* (Fig. 3*a*), and *Pseudochromis* the circumorbital series are similar though the preorbital covers relatively less of the surface of the head.

Jaws. The jaws and jaw teeth in *Epinephelus, Pseudogramma,* and *Plesiops* are similar. The gape is wide and the maxillary extends behind the eye; the pedicel of the premaxillary is shorter than the toothed portion; the maxillary extends well beyond the premaxillary maxillary and has a splintlike supramaxillary on its straight upper border (Figs. 3*a, b*); many of the teeth are depressible; and the teeth in the lower jaw extend well behind those of the upper and are

FIG. 3. First three circumorbital bones, nasals, premaxillaries, maxillaries, and supramaxillaries; teeth not shown. *a, Plesiops,* right side, with the nasal organ indicated; *b, Pseudogramma,* left side.

in two or more rows throughout. In *Pseudochromis* the jaws are shorter and the teeth are all rigid; the premaxillary pedicel is at least as high as the toothed portion; the maxillary curves down around the end of the premaxillary and lacks a supramaxillary; and the teeth in the lower jaw are in a single row laterally. The teeth on the vomer, palatines, and pharyngeals of *Pseudochromis* are all rigid, as compared to the partly depressible teeth on these bones in the other three genera.

Suspensorium. The chief difference in the suspensoria of the four genera studied seems to be that the palatine of *Pseudochromis* is loosely articulated (apparently by ligament) to the rest of the structure, whereas in the other three it is rigidly united by suture to the ectopterygoid and mesopterygoid (Fig. 5).

TABLE 2

TAXONOMIC TREATMENT OF CERTAIN PERCOID GROUPS BY VARIOUS AUTHORS

SMITH, 1949, 1953, 1954*a*, 1954*b*	WEBER and DE BEAUFORT, 1929, 1931	REGAN, 1913	NORMAN, 1957	SCHULTZ, 1953
Pseudogrammidae	to Serranidae	to Serranidae	to Serranidae	Pseudochromidae
Pseudochromidae				
Pseudochrominae				
Pseudoplesiopsinae	Pseudoplesiopidae	Pseudoplesiopidae	Plesiopidae	
Plesiopidae	Plesiopidae	Plesiopidae		
Acanthoclinidae	Acanthoclinidae		Acanthoclinidae	
Anisochromidae	—	—	—	—

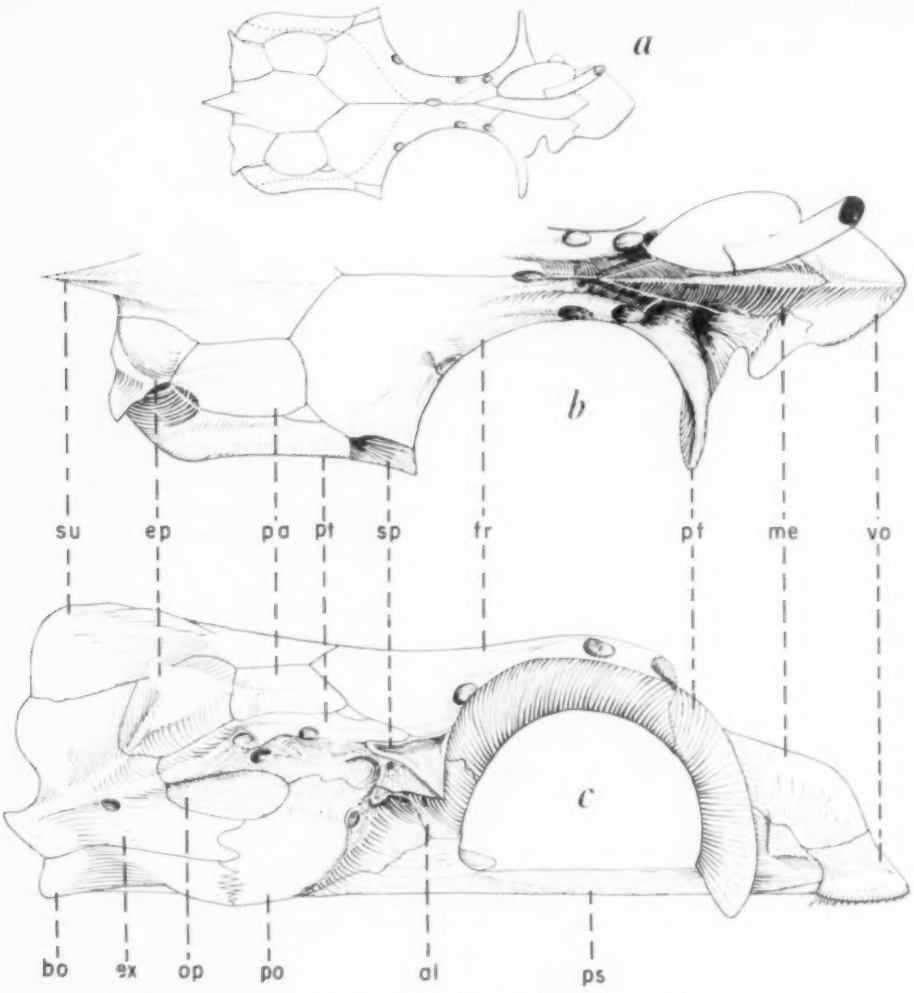

FIG. 4. *Pseudogramma. a* and *b*. Top views of the skull, with the left nasal bone in position, *a* showing the inner borders of the infraosseous portion of the supraorbital lateral line canals by dashes; *c*, side view of skull. al, Alisphenoid; bo, basioccipital; ep, epiotic; ex, exoccipital; fr, frontal; me, mesethmoid; op, opisthotic; pa, parietal; pf, prefrontal; po, prootic; ps, parasphenoid; pt, pterotic; sp, sphenotic; su, supraoccipital; vo, vomer.

Opercular Bones. The preopercle of *Epinephelus* is serrate. In *Pseudogramma* the edge is membranous except for the single enlarged spine (Fig. 5). In *Pseudochromis* the entire edge is membranous. In *Plesiops* the preopercle has a double border reminiscent of that appearing externally in some of the apogonids, but neither of these borders is serrate.

In *Epinephelus* the opercle has three superficially visible spines. In *Pseudogramma* (Fig. 5) these spines have become rudimentary and are concealed, but they can still be made out

when the opercle is cleaned. The opercle of *Plesiops* ends in a frayed membrane and that of *Pseudochromis* is rounded posteriorly.

Hyoid Arch. There are seven branchiostegal rays in *Epinephelus, Pseudogramma* (Fig. 6), *Aporops,* and *Suttonia;* six in *Plesiops* and *Pseudochromis.* The branchiostegal membranes are broadly attached to the isthmus in *Pseudochromis,* attached far forward to one another but more or less free from the isthmus in the other genera. In *Plesiops* alone the third branchiostegal ray is considerably larger than those before and behind it.

Gill Arches. In all four genera skeletonized there is a pseudobranch, and the cleft behind the fourth gill arch is considerably restricted. In all, there is one pair of dentigerous lower and three pairs of toothed upper pharyngeals. In *Epinephelus* and *Pseudochromis* the gill rakers are fairly normal; the gill rakers of *Pseudogramma* and *Plesiops,* however, are in the form of flat plates at the ends of the arch with spiny knobs toward the central portion.

Pectoral Girdle. The pectoral girdle in all four genera is similar (Fig. 7) despite the fact that externally *Pseudogramma* appears to have a lobate pectoral base. In all, a long extension of the coracoid runs downward and forward to meet the cleithrum. There are two postcleithra. The forward tip of the pelvic girdles articulate with pads on the inner surfaces of the cleithra. One and a half actinosts join the coracoid and two and a half meet the scapula, though the relationship is more nearly one and three in *Pseudochromis.* The most notable difference would appear to be that there is a curious downwardly projecting hook (or, viewed conversely, an embayment) in the outer surface of the cleithrum of *Plesiops* below.

Pelvic Girdle. The pelvic girdle in all four genera consists primarily of struts between the pelvic fins and the cleithra (Fig. 7). Those of *Pseudogramma* are surprisingly strong and are longer than the pelvic fins themselves.

Vertebral Column. The number of vertebrae for several species of *Epinephelus* given by Boulenger (1895: 115) is 24. The vertebrae in *Pseudogramma* (including the terminal half-

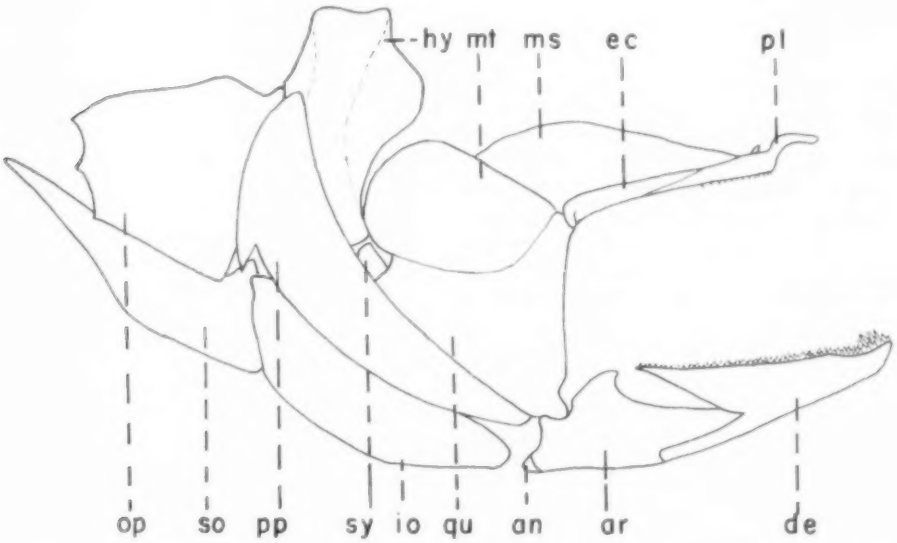

FIG. 5. Right suspensorium and lower jaw of *Pseudogramma,* external view. an, Angular; ar, articular; de, dentary; ec, ectopterygoid; hy, hyomandibular; io, interopercle; ms, mesopterygoid; mt, metapterygoid; or, opercle; pl, palatine; pp, preopercle; qu, quadrate; so, subopercle; sy, symplectic.

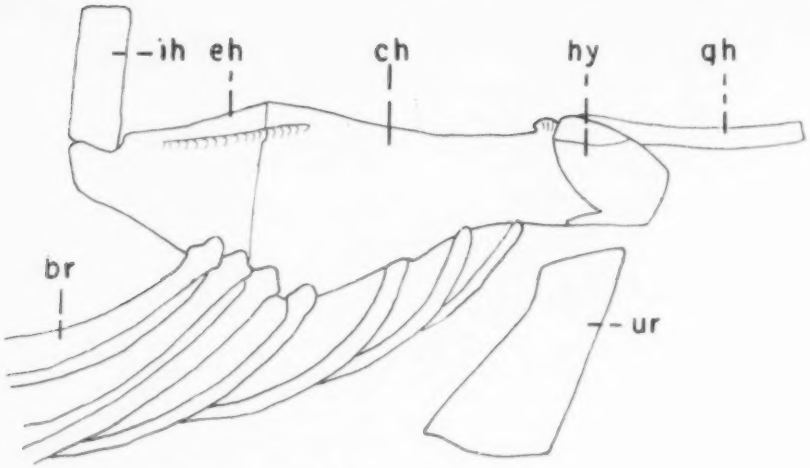

FIG. 6. Right half of hyoid apparatus of *Pseudogramma*, external view with the urohyal dislocated. br, Branchiostegal ray; ce, ceratohyal; eh, epihyal; gl, glossohyal; hy, hypohyal; ih, interhyal; ur, urohyal.

vertebra) number 26, in *Plesiops* 25, and in *Pseudochromis* 26. The first interneural in *Pseudogramma, Plesiops,* and *Pseudochromis* extends between the second and third neural arches; *Epinephelus* was not examined for this character.

In *Epinephelus* and *Pseudogramma* the second interhaemal is very strong and runs up to wedge into the posterior face of a haemal arch. In *Plesiops* and, especially, *Pseudochromis,* the second interhaemal is considerably weaker.

Caudal Skeleton. The caudal skeleton of all four genera appears to be built on the same plan (Fig. 8), though there is considerable minor variation, especially in the amount of fusion. Thus there may be two or three epurals and three to five hypurals.

Summary of Internal Differences. Though the internal, especially the osteological, differences between *Epinephelus, Pseudogramma, Plesiops,* and *Pseudochromis* are slight, they are not entirely negligible. Thus each of the three serranid offshoots stands apart in one fashion or another.

Pseudogramma differs from the other genera in the enlarged nasal organ, the preopercular spine with its associated glandular area, and in having two pyloric caecae.

Plesiops appears hardest to define on the basis of internal features. Perhaps the hook on the anterior face of the cleithrum and the double border to the preopercle are the most salient.

Pseudochromis differs immediately from the others in the mouth parts. The teeth are rigid; the maxillary bends around the premaxillary and lacks a supramaxillary; the premaxillary pedicels are elongate; and the palatines are movably articulated with the remainder of the suspensorium.

External Features. With one exception the external features of the fishes investigated will not be treated on a genus–to–genus basis as they have been noted by every ichthyologist who has worked with these groups. However, some of them will be taken up in the discussion of relationships in the next section.

The exception concerns the number of branched caudal rays. The perciform fishes are often stated to have 15 or fewer branched caudal rays. In *Epinephelus* the usual 15 were counted in 3 specimens. However, 16 are present in the one specimen available of *Grammistes.* The stained specimen of *Pseudogramma* has 17, as does that of *Pseudochromis.* In the 5 available specimens of *Plesiops,* one has 15, one 16, and three 17.

TAXONOMIC TREATMENT OF THE "PSEUDOGRAMMIDS"

The above review has indicated that there is little basic osteological difference between the serranids, "pseudogrammids," and "pseudochromids." Nevertheless there seems to be one group, traditionally included in the Serranidae, that seems to be far more closely related to the "pseudogrammids" than either *Epinephelus* or the "pseudochromids." This is the "Grammistinae" containing the genera *Rypticus, Grammistes, Pogonoperca,* and *Grammistops* Schultz, 1953 (which equals *Tulelepis* Smith, 1954). Indeed, upon analysis of the 14 characters listed in Table 3, the "pseudogrammids" fall with the "pseudochromids" rather than with the "Grammistinae" only in the lateral line and scale structure.

If the "Grammistinae" is enlarged to include the "pseudogrammids," the old distinction of this "subfamily" from the other serranids by the flap connecting the upper portion of the gill cover to the body can be retained, for this feature applies also to the "pseudogrammids." The two groups combined may be defined as follows (though it should be noted that the included genus *Pogonoperca* has not been examined):

Whole upper border of opercle attached to the body by a flap of skin. Nasal organ dorsoventrally elongate, made up of a number of

TABLE 3

COMPARISON BETWEEN "GRAMMISTINAE," "PSEUDOGRAMMIDS," AND "PSEUDOCHROMIDS"

CHARACTER	"GRAMMISTINAE"	"PSEUDOGRAMMIDS"	"PSEUDOCHROMIDS"
Operculum	joined to the skull by a membrane above	joined to the skull by a membrane above	free from the skull above
Maxillary	large, with a supramaxillary	large, with a supramaxillary	moderate to small, with or without a supramaxillary
Teeth	in bands, many depressible	in bands, many depressible	usually rigid and in one row on the lower jaw posteriorly
Nasal organ	in *Grammistes*, of numerous lamellae	of numerous lamellae	small, with few lamellae
Opercle	with 3 spines	with spines reduced, not visible externally	without spines
Preopercle	usually with 1 to 4 spines above	with 1 specialized spine above	without spines
Branchiostegal rays	6 or 7	7	6
Opercular scales	small, similar to those on body	small, similar to those on body	somewhat to greatly enlarged
Body scales	embedded, in *Grammistes* with concentric rings	about as in *Epinephelus*	about as in *Epinephelus*
Lateral line	single, complete	incomplete or interrupted	incomplete or interrupted
Dorsal and anal spines	when present, the last shorter than the penultimate	the last shorter than the penultimate	when present, the last longer than the penultimate
Dorsal and anal soft rays	basally embedded in fatty tissue in adult *Rypticus* and *Grammistes*	basally embedded in fatty tissue in adult	not embedded in fatty tissue in adult
Inner pelvic ray	attached to abdomen by a membrane	attached to abdomen by a membrane	entirely free from abdomen
Pyloric caeca	1 or 2	1 or 2	none

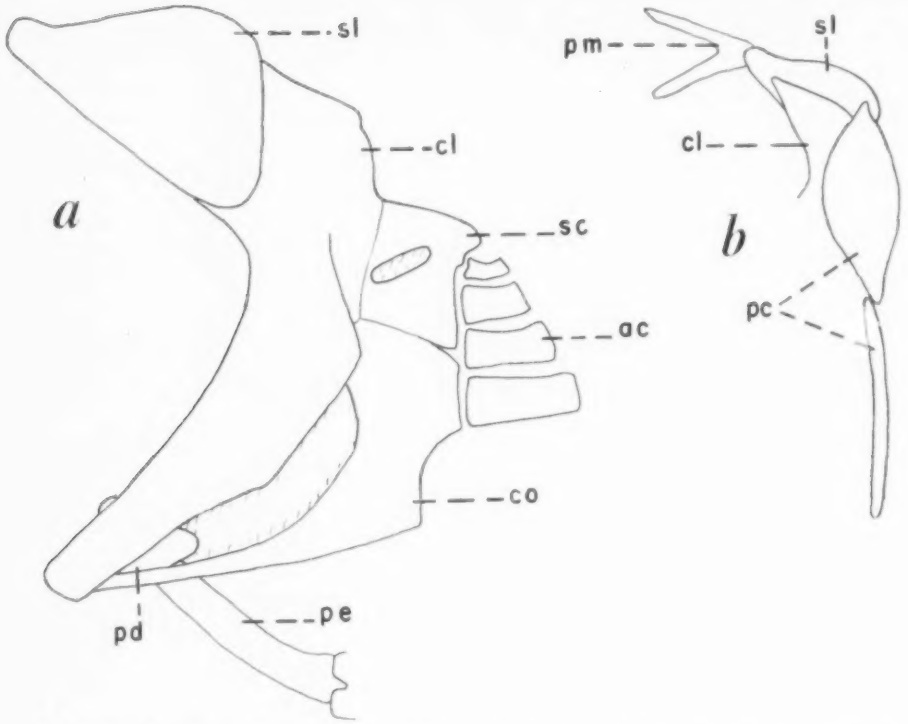

FIG. 7. *Pseudogramma. a,* Lower portion of left pectoral and pelvic girdles, from outside; *b,* upper and inner portions of right pectoral girdle, from inside and drawn to about half the scale of *a.* ac, Actinost; cl, cleithrum; co, coracoid; pc, postcleithra; pd, pad on cleithrum for articulation with pelvic girdle; pe, pelvic girdle; pm, posttemporal; sc, scapula; sl, supracleithrum.

nearly parallel, longitudinally oriented lamellae (instead of the usual rosette). Mouth large; supramaxillary present. Teeth mostly villiform, many of them depressible. No enlarged scales on operculum. Upper portion of preopercular border usually with one to four projecting spines. Two (or one) pyloric caeca. Dorsal spines II to VIII. Anal with no or with III spines, in the latter instance with the last spine shorter than the penultimate. Pelvics I, 5, the inner ray attached to the abdomen by a membrane.

The group of genera defined above seems to be sufficiently distinctive to warrant family recognition. That they are all interrelated is indicated by the rather large number of presumably independent minor characters held in common. That they deserve family rather than subfamily status is a more open question, and the author admits to considerable vacillation on this matter.

The major points in favor of family recognition would seem to be the following: (1) The genera here attributed to the Grammistidae appear to be easily and clearly distinguishable from all other percoid fishes. If intermediates exist between them and other families, they have escaped the author's notice. Apparently the closest relatives are certain members of the Serranidae, e.g., *Diploprion,* with somewhat elongate nasal organ and membranes between the pelvics and the abdomen. However, in other characters *Diploprion* falls clearly with *Epinephelus* rather than with the grammistids. (2) Although the characters differentiating the

FIG. 8. Caudal skeleton of *Pseudogramma;* interosseous spaces hatched.

grammistids from related families are morphologically rather trivial, they are no more so than the features distinguishing many percoid families. In the percoids, the only alternative to such a basis of separation would appear to be the lumping of thousands of species into one or a few unwieldy families. (3) The Serranidae is already such a family. Indeed Weber and de Beaufort (1936: 555–559) have found it necessary to separate out the Serranidae at seven different points in their key to the Indo-Australian percoid fishes. Any procedure that would remove one or more of the heterogeneous elements now contained in the Serranidae would make the serranids a more manageable and more meaningful group. (4) The genera here included in the Grammistidae represent a phylogenetic lineage of respectable size. Recognition of the Grammistidae is therefore a somewhat different and, in the author's opinion, a more worthy procedure than chipping off as separate families the most aberrant endpoints of lineages. (5) From a purely practical standpoint, the retention of the grammistids, including the "pseudogrammid" genera, as a subfamily of the Serranidae would make it impossible to use the incomplete or interrupted lateral line as a basis for separating the serranids from the "pseudochromid" groups.

Nevertheless, one very valid argument can be given for retaining subfamily rank for the grammistids: that changes in status of portions of the Serranidae should not be undertaken without a consideration of the family as a whole. The author gladly admits the point. He merely feels that waiting for anything like a comprehensive review of the Serranidae is an impractical procedure.

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Pinnixa darwini, a New Species of Pinnotherid Crustacean from the Galapagos Islands

JOHN S. GARTH[1]

WHILE REPORTING on the Crustacea Decapoda Brachyura of the Lund University Chile Expedition (Garth, 1957), the writer had occasion to review the status of the genus *Pinnixa* White on the west coast of South America, and, particularly, to re-examine specimens previously referred by various authors to *P. transversalis* (Milne Edwards and Lucas, 1842: pl. 10, figs. 3, 3a–e; 1844: 23). This proved to be a quasi-generic designation, or at least a species complex under which two or more valid species had been masquerading. It is not surprising, therefore, that when specimens from Darwin Bay, Galapagos Islands, so reported by the writer (Garth, 1946: 497), together with certain other Galapagos material more recently acquired, came under the same close scrutiny, it was discovered that in addition to the aforementioned *P. transversalis*, which has as its type locality the shores of Chile, a new and perhaps endemic species was represented among them. It being deemed inappropriate to include a Galapagos Islands species in a report on the fauna of Chile, its description was withheld at the time and is now presented in connection with the world-wide observance of the Darwin Centennial, the 100th anniversary of the publication in 1859 of "The Origin of Species."

Although Charles Darwin is not known to have collected decapod crustaceans in the Galapagos Islands, or elsewhere along the west coast of South America, during the celebrated voyage of the *Beagle*, his monograph on the Cirripedia (1851–1854) was a fundamental contribution to crustacean systematics. Had his genius for elucidating the obscure been directed toward the crabs instead of toward the barnacles, our present knowledge of the Pinnotheridae, a family of brachyurans living as commensals with polychaetes, mollusks, and echinoderms, would have been immeasurably enriched. The revelation of their fascinating habits was left to a later group of nineteenth century investigators, notably Verrill (1870), who referred to them quaintly, although not too correctly, as parasites. However, in view of Darwin's contribution to systematic carcinology and to Galapagan zoogeography, it seems entirely appropriate that a new species of pinnotherid crustacean from the bay that bears his name and the islands to which he brought lasting fame should be dedicated to the illustrious proponent of evolutionary theory and exponent of natural selection.

Family PINNOTHERIDAE Dana
Genus PINNIXA White
Pinnixa darwini, n. sp.
Fig. 1A–F

TYPE: Male holotype and ovigerous female allotype, A.H.F. No. 3812a and b, respectively, from Darwin Bay, Tower Island, Galapagos Islands, 40–70 fathoms, January 16, 1938, collected by the "Velero III" at station 783–38. Male paratype, same locality, date, and station number, to be deposited in the collections of the U. S. National Museum.

MEASUREMENTS: Male holotype, length 3.1 mm., width 5.8 mm., frontal width 0.9 mm., fronto-orbital width 2.15 mm., cheliped (ischium-merus-carpus 1.6 mm., manus-dactylus 3.0 mm.) 4.6 mm., chela 3.0 mm., superior margin 1.8 mm., height of palm 1.6 mm., dactyl 1.5 mm., merus of leg three: length 2.8 mm., width 1.2 mm. Female allotype, length 3.8 mm., width 8.2 mm.

DIAGNOSIS: Cardiac ridge obsolescent; anterolateral margins forming a sharp, milled crest. Eyes and eyestalks large, filling orbits. Propodus of external maxillipeds short and broad, dactylus considerably longer. Chelae moderately robust, fingers enclosing an oval gape. Merus of

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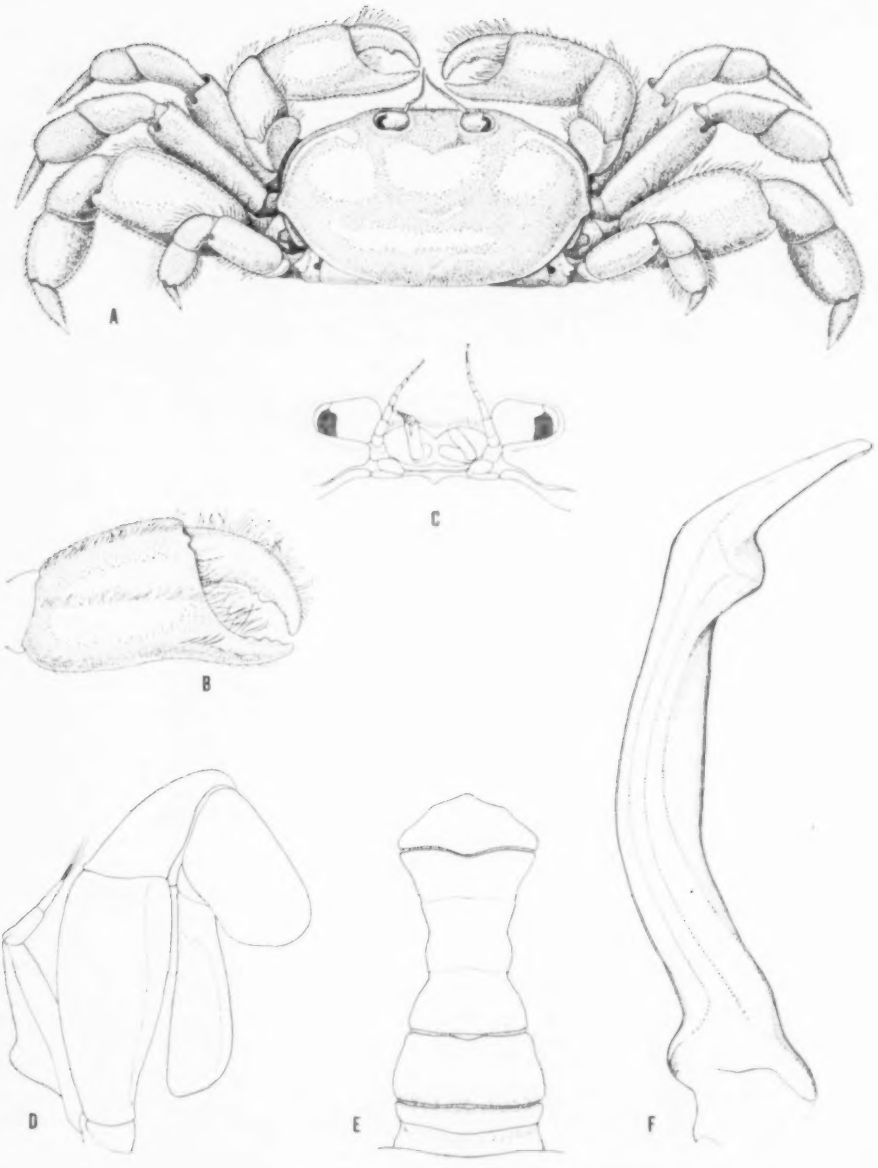

FIG. 1. *Pinnixa darwini*, male holotype, A.H.F. No. 3812a, station 783–38. A, dorsal view, × 8; B, right chela, × 12; C, frontal view, × 17.5; D, right outer maxilliped, × 30; E, abdomen, × 12; F, first pleopod, × 45. D–F with fringing hairs omitted. A–E drawn by Russel Cangialosi; F drawn by Anker Petersen.

leg three two and one-third times as long as wide; leg four not overreaching merus of leg three. Male abdomen terminally broadened, tip triangular. Male first pleopod with a terminal projection and a subterminal swelling.

DESCRIPTION: Carapace suboblong, width 1.87 times length in male, 2.16 times length in female, lateral angles forming prominent shoulders from which sides drop away steeply, surface smooth and porcellanous, minutely punctate, and laterally fringed with plumose hairs. Gastrocardiac trench shallow, cardiac region elevated but uncrested, anterolateral margins, from lateral angle of carapace to cervical suture, forming a continuous, sharply defined, granular crest. Front truncate, slightly advanced beyond orbits, bilobed, lobes fringed. Orbits wide, inclined transversely in dorsal view, somewhat obliquely in frontal view, and completely filled with unconstricted eyestalk and cornea.

External maxilliped with a short, broad propodus and a longer, spatulate dactylus broadening distally; all segments with fringing hairs.

Chelipeds of male well developed, merus trigonal, inner surface concave; carpus smooth and, like merus, hairy; manus widening distally, height .88 times superior length, uncrested, hairs of outer surface arranged principally in three rows, the lower extending onto pollex, the middle terminating at gape, and the upper continuing on dactyl; fingers arching toward each other, pollex with three denticles, lower margin of hand sinuous; dactylus with two small teeth at middle of gape; gape choked with clavate hairs.

Dactyls of ambulatory legs one and two straight and slender, of leg three broad and slightly curved, of leg four broad and straight. First leg narrower than, and reaching middactylus of, second; second leg reaching midpropodus of third; third leg longest, merus 2.33 times long as wide, carpus and propodus correspondingly broadened, fourth leg greatly reduced, its merus not over half the length of, its dactyl not overreaching, the merus of leg three. All legs conspicuously hairy.

Male abdomen with somites four to six fused, edges sinuous; broadest at base of somite three, narrowest at base of somite five, broadening again to base of somite seven; seventh somite triangular in outline. Line of hair on somite two continued across sternum.

Male first pleopod with a spinelike terminal process bent at a slight angle to the axis of the appendage; a bulbous subterminal swelling beneath.

Carapace of female broader than male, side walls less steep, shoulder less prominent; chelae more slender than male, palm narrower, fingers longer, gape less apparent.

REMARKS: At the time of publication of the "Littoral brachyuran fauna of the Galapagos Archipelago" (Garth, 1946), but one species of *Pinnixa, P. transversalis* (Milne Edwards and Lucas) was known to inhabit the Galapagos Islands. The basis for this record, and for the diagnosis and figures presented (*ibid.*: 498, pl. 84, figs. 6 and 8) was a male and female from Darwin Bay, Tower Island, 40–70 fathoms, "Velero III" station 783–38, identified by the late Steve A. Glassell, together with the tubes of *Chaetopterus variopedatus* (Renier) from which they were taken. Subsequently, two other lots of *Pinnixa* from the Galapagos Islands, both of Hancock expeditions origin, have come to hand: the first, a single male from Tagus Cove, Albemarle Island, 12 fathoms, December 10, 1934, "Velero III" station 330–35, identified by the late Mary J. Rathbun as *P. transversalis*, and the present group of two males and one ovigerous female, which, although coming from the same locality and station as the Glassell-identified specimens, represent a totally different and hitherto undescribed species.

The proposed new species finds its most closely related species in *Pinnixa faxoni* Rathbun (1918: 133, pl. 29, figs. 4–7, figs. 77a, b), type locality Trinidad, of which it is almost certainly the Pacific analogue. According to Dr. F. A. Chace, Jr., curator of marine invertebrates, U. S. National Museum, who made the comparison, the carapace, including the ridge across the hinder part, is practically identical with some of the type series of *P. faxoni*. Only three important differences between the two species were noted: first, the fingers of the chelae gape much more widely in the Galapagos species than in *P. faxoni*, those of the male of *P. faxoni* being very much like those of the female of the proposed new species, those of the female of *P.*

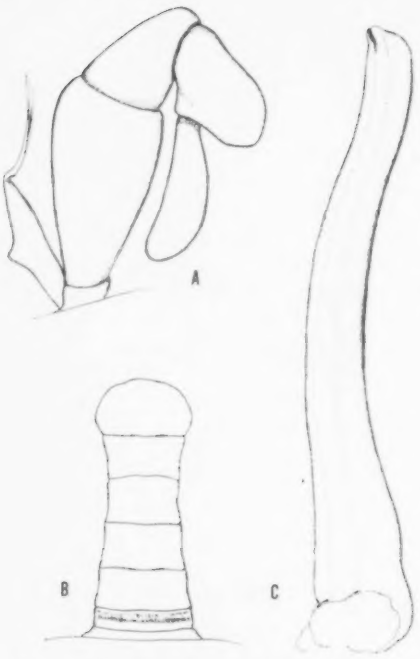

FIG. 2. *Pinnixa transversalis* (Milne Edwards and Lucas), male, station 783–38. A, right outer maxilliped, × 20; B, abdomen, × 6; C, first pleopod, × 26. Fringing hairs omitted. Drawn by Anker Petersen.

faxoni meeting throughout their lengths; second, the male abdomen of the new species is more constricted in the central portion and more abruptly broadened distally than in *P. faxoni* (as shown in Rathbun's figure 77a); third, the male first pleopods are different in the two species, the distal, spinelike process in *P. faxoni* being much longer, more slender, and bent at nearly a right angle to the axis of the appendage. Furthermore, *P. faxoni* is apparently the shaggier of the two species, but how much so cannot be determined because of the matting of the hairs in the type series of *P. faxoni* with fine silt.

Pinnixa transversalis (Milne Edwards and Lucas) from the same locality (Fig. 2A–C) may be distinguished from the new species by the shape of the male abdomen, which is unconstricted medially and has a rounded terminal segment, by the external maxilliped, the propodus of which is less quadrate, and by the male first pleopod, which lacks the spinelike extension with its bulbous base. The specimen from which these figures were made measures 4.8 mm. in length and 9.4 mm. in width and is without doubt the 5.0 × 9.4 mm. specimen, erroneously recorded as a female (Garth, 1946: 498), of which measurements were given, since the female from the same station measures only 3.3 × 6.8 mm. In addition, *P. transversalis* has a sharp ridge extending entirely across the posterior portion of the carapace, and the chelae in both sexes are narrow, thin, and straight, the fingers pointed.

Finally, it should be stated that, while the specimens of *Pinnixa transversalis* were recovered from the arenaceous tubes of *Chaetopterus*, the commensal host of the new species remains a subject for future investigation.

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On the World-wide Dispersal of a Hawaiian Barnacle, *Balanus amphitrite hawaiiensis* Broch[1]

HUZIO UTINOMI[2]

IN RECENT YEARS a great deal of attention has been given by many workers, especially by marine ecologists and oyster planters, to the introduction of an Australian barnacle, *Elminius modestus* Darwin, into British waters and to its subsequent rapid spread along the continental European coasts from Brittany to the mouth of the Elbe River. The most recent extensive reviews of the occurrence of this barnacle on those coasts have been given by Den Hartog (1953) and Kühl (1954). Similarly, another instance of the introduction of an adventive barnacle into British coastal waters has also focused more attention on the possibility of other importations of many harmful foreign animals, as well as the extension of their natural geographical distribution. These studies strongly suggest that transportation on ships' bottoms or as stowaways among oysters is the chief means of migration (Allen, 1953; Coe, 1956).

The second example of a barnacle imported into European waters has long been considered to be *Balanus amphitrite* var. *denticulata* Broch, which was originally described by Broch (1927) from the Suez Canal. Since the first record of its occurrence on the southern coasts of Britain by Bishop (1950), most of the European workers, especially field ecologists who are not acquainted with the Pacific species of barnacles, have overlooked the fact that it is identical with *Balanus amphitrite* forma *hawaiiensis* Broch (1922), which is thought to be native to the Hawaiian Islands.

The object of this paper is to state the reasons for considering both of these forms as identical, at least with each other and possibly with other forms (or subspecies); and to present the alleged distribution of these related forms, as far as can be determined from the records of their occurrence.

ACKNOWLEDGMENTS

I am especially indebted to Mr. William A. Newman, Pacific Islands Central School, Truk, East Caroline Islands, for data of occurrence in America, and to Mr. Kasio Ota, Zoological Institute, Agriculture Faculty, Hokkaido University, for information on habitats. Thanks are also due to Dr. Masaru Kato, Zoological Institute, Kyoto University, for translating a Russian paper.

IDENTITY OF SUBSPECIES *denticulata* WITH SUBSPECIES *hawaiiensis*

Balanus amphitrite Darwin (1854) comprises many local forms, occasionally treated as either "subspecies" or "varieties," which are diversified in the number of teeth on the labrum. Most of the subspecies have only three teeth on each side of a median notch. The other subspecies almost always have four teeth, or a larger number (Hiro, 1938). Even in the subspecies having three or four teeth, the actual number is apt to vary among specimens, but in such cases the innermost one is either small or only rudimentary.

The two subspecies, *hawaiiensis* and *denticulata*, have such a multidenticulate labrum. The same is true of *Balanus eburneus* Gould and of *B. improvisus* Darwin, which are found as migrants on ships sailing between America and Europe. The number of teeth is also variable, ranging between 8 and 20; in most cases 10 to 13 larger teeth are found on each side, but never fewer than 8.

The most outstanding features in external ap-

[1] Contributions from the Seto Marine Biological Laboratory, No. 335. Manuscript received January 2, 1958.

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pearance which prove the identity of both forms are the colored stripes on the wall and the shape of the opercular valves. The shell is glossy white, smooth, and furnished with dark violet longitudinal stripes not crossed by any transverse stripes, though growth lines are faintly defined. Usually a broad white area is present in the middle of the larger compartments (carina, laterals, and rostrum), and a similar white area is present along both sides, the colored stripes being indistinct or quite absent there (see Table 1). The parietal tubes (the number of which corresponds with the number of the colored stripes, both distinct and obsolete) are narrow and numerous; the longitudinal septa on the inner lamina are strongly developed and run up to the sheath as high ridges which are very finely denticulate on both sides. The radii are very broad, with summits almost parallel to the base (Fig. 1).

In describing the new variety *denticulata* from the Suez Canal, Broch (1927) did not mention its close affinity with his earlier form *hawaiiensis* described in 1922. A comparison of his descriptions and figures of both forms with the Japanese specimens of *hawaiiensis* clearly shows that there is no difference important enough to separate them as different subspecies. Therefore, I believe that *denticulata* must be the same as *hawaiiensis*.

DIFFERENCES BETWEEN SUBSPECIES *hawaiiensis* AND SUBSPECIES *communis*

Notwithstanding the peculiarities mentioned above, sometimes there has been confusion among cirripede systematists between forma *hawaiiensis* (or *denticulata*) and Darwin's variety *communis* (see Table 3).

For example, Nilsson-Cantell (1938: 37) recognized both subspecies as distinct, but mentioned that "I do not consider it impossible that they (*denticulata*) represent a special race from the canal zone, but I do not think that numerous teeth on the labrum are a special characteristic of the subspecies *denticulata*." He emphasized that a great variability in the number of teeth on the labrum is not always of systematic importance, remarking that "the typical *communis* also has numerous teeth on the labrum." However, I most emphatically dissent from his opinion in this respect. As he says, it is true that the balanids are highly variable as far as a particular character is concerned, but I hold that there are certainly some admittable limitations in the range of variation. A similar unreliability in identifications based only on the labrum was pointed out by Pilsbry (1916: 88), in the case of *Balanus improvisus*.

Some specimens of subspecies *communis* resemble subspecies *hawaiiensis* superficially, being often found together in the same place, but

TABLE 1

THE NUMBER OF LONGITUDINAL COLORED STRIPES IN ALL COMPARTMENTS OF *Balanus amphitrite hawaiiensis* AND *Balanus amphitrite communis*[*]

SIZE OF SPECIMENS	CARINA	LEFT CARINO-LATERAL COMPARTMENT	RIGHT CARINO-LATERAL COMPARTMENT	LEFT LATERAL COMPARTMENT	RIGHT LATERAL COMPARTMENT	ROSTRUM
B. a. hawaiiensis						
c.r.d. 15.4 mm.	(0)5(1)5(1)	(1)2(1)	(0)2(2)	(1)4(2)4(1)	(0)5(1)4(2)	(2)5(2)5(2)
c.r.d. 18.0 mm.	(1)3(2)4(1)	(1)2(1)	(1)2(2)	(2)4(2)4(1)	(1)5(2)4(2)	(2)5(3)6(1)
c.r.d. 18.5 mm.	(0)5(2)4(0)	(0)3(1)	(1)2(1)	(2)5(1)3(1)	(1)4(1)4(0)	(2)4(2)4(3)
c.r.d. 19.6 mm.	(2)4(1)3(1)	(1)2(1)	(1)2(1)	(1)3(3)4(2)	(2)2(2)2(0)	(1)5(2)4(2)
B. a. communis						
c.r.d. 14.0 mm.	10	3	2	10	9	9
c.r.d. 18.2 mm.	8	2	2	9	9	9
c.r.d. 20.0 mm.	9	4	2	10	10	10

[*] c.r.d. = carino-rostral diameter. Numbers without parentheses represent distinct stripes. Numbers in parentheses represent obsolete or reduced stripes. The total number corresponds with the number of parietal tubes in each of the compartments.

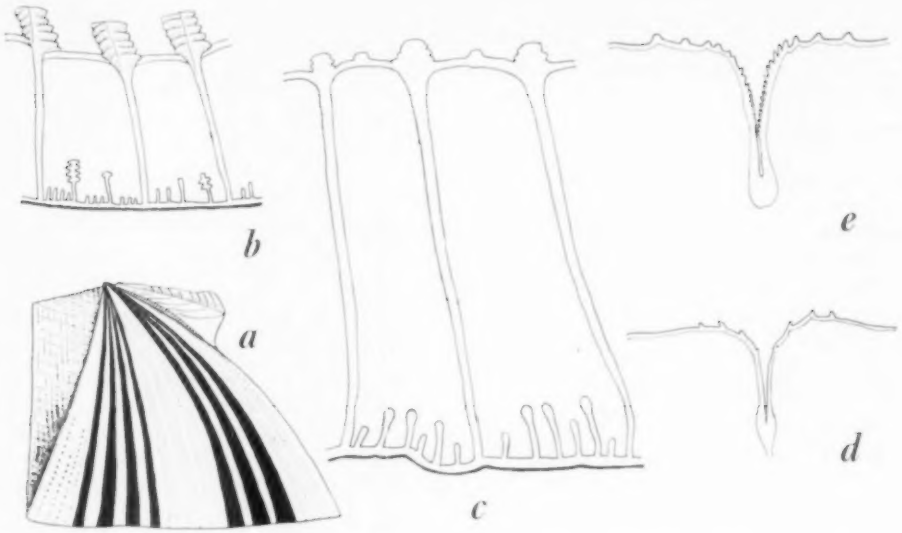

FIG. 1. *Balanus amphitrite hawaiiensis* Broch (*a*, *b* and *c*) and *B. amphitrite communis* Darwin (*d*): *a*, Profile of left lateral compartment, showing the arrangement of longitudinal colored stripes, either distinct or indistinct (dotted in the figure); *b*, *c*, basal view of parietal tubes; *d*, *e*, labrum.

the two differ in several important details of structure, as summarized in Table 2.

Consideration of these characteristics will prove that the two subspecies are separable from each other when large series of specimens are examined.

DISTRIBUTION AND SYNONYMY

Herewith is presented a summary of accounts of the corresponding subspecies of *Balanus amphitrite* Darwin given by previous workers and the supposed geographical distribution of *B. amphitrite hawaiiensis* Broch (Fig. 3). The evidence is far from complete and some records of occurrence are not conclusive, since most of the subspecies or forms of *Balanus amphitrite*, especially the most familiar *communis*, have been insufficiently described (often without detailed figures), or are recorded only by a subspecific name. Nevertheless, those I have listed may help future workers towards the solution of the problems presented herein.

1. Recorded as *B. a. hawaiiensis:*

Kaladis Point, Mindanao (Broch, 1922).
Pearl Harbor, Hawaii (Broch, 1922).
Honolulu Harbor, Hawaii (Pilsbry, 1928).
Sasebo, Kure, Maizuru, Seto, and Misaki, Japan (Hiro, 1937, 1938).
Persian Gulf (Nilsson-Cantell, 1938).
Suo, Kiirun, Tansui, Takao, and Mako, Formosa (Hiro, 1939).
Aio, Seto Inland Sea, Japan (Hudinaga and Kasahara, 1942).
Pearl Harbor and Kaneohe Bay, Hawaii (Edmondson and Ingram, 1939; Edmondson, 1946).
Misaki, Japan (Hirano and Okushi, 1952).

2. Recorded as *B. a. denticulata:*

Suez Canal (Broch, 1927; Ciurea *et al.*, 1933; Monod, 1937).
Southern coasts of Britain (Bishop, 1950; Norris *et al.*, 1951; Crisp and Molesworth, 1951).
Atlantic coasts of France (Bishop *et al.*, 1957).
Knysha Estuary, South Africa (Millard, 1950).

Queensland and Torres Strait, Australia (Allen, 1953).
Durban Bay, South Africa (Day and Morgan, 1956).

3. Recorded as *B. a. communis* (in part):
Ismailia, Timsah Sea, Suez Canal (Nilsson-Cantell, 1921).
? Billiton, Sunda Islands (Nilsson-Cantell, 1921).
? Messina port, Italy (Nilsson-Cantell, 1921).
Istanbul harbor, Turkey (Neu, 1939).
Middle Harbor, Port Jackson, Australia (Pope, 1945).
Adriatic Sea (Kolosváry, 1947).
Black Sea (Zevina and Tarasov, 1957).

4. Recorded as *B. a. venustus:*
Krusadai, Gulf of Manaar, Ceylon (Raj, 1927).

5. Recorded as *B. a. franciscanus* and *B. a. herzi:*
San Francisco Bay, California (Rogers, 1949).[3]

6. Recorded as *B. amphitrite,* subspecific name not given:
Atlantic coasts of France (Prenant, 1929; Fischer, 1929; Fischer-Piette, 1932, etc.).
? Biscayne Bay, Florida (Weiss, 1948).
Oakland Estuary, California (Graham and Gay, 1945).

7. Unpublished records of occurrence:
San Diego, Salton Sea, and San Francisco Bay, California; and the Hawaiian Islands (Newman, 1955, 1956: personal communication).
Dakar, West Africa (from I.F.A.N. Collection).
Seto Inland Sea and Ise Bay, Japan (Ota, 1955: personal communication).

A detailed discussion of the synonymies listed above is omitted, for the sake of saving space, but the preceding illustrations and descriptions

[3] I am not certain whether another new subspecies, *B. a. saltonensis* Rogers, from the Salton Sea, is the same as the others or is distinct from them.

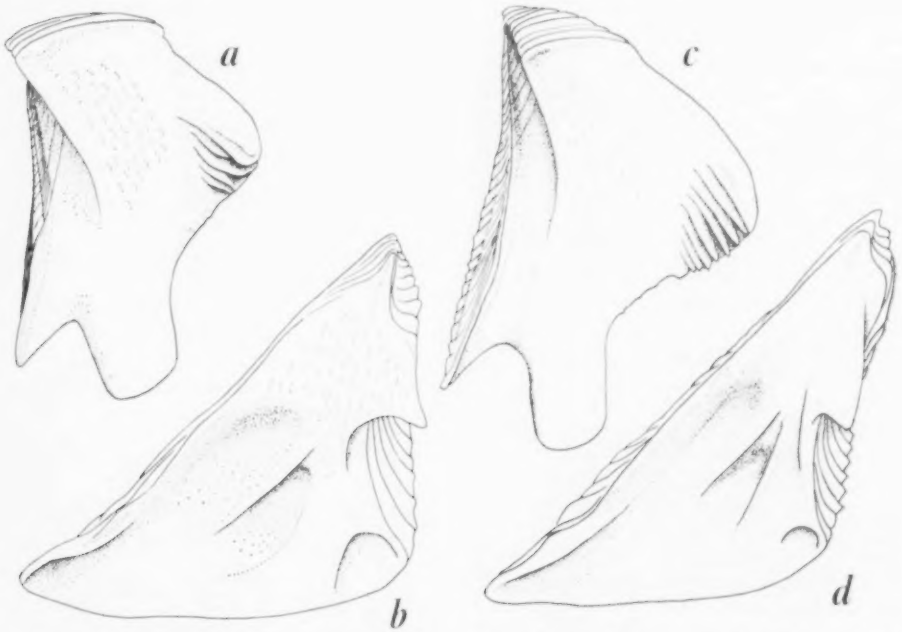

FIG. 2. *Balanus amphitrite hawaiiensis* Broch (*a* and *b*) and *B. amphitrite communis* Darwin (*c* and *d*): *a* and *c*, Inside of tergum; *b* and *d*, inside of scutum.

TABLE 2

DIFFERENCES IN DETAILS OF STRUCTURE BETWEEN *Balanus amphitrite hawaiiensis* AND *B. amphitrite communis*

DETAILS OF STRUCTURE	*B. amphitrite hawaiiensis*	*B. amphitrite communis*
Ground color of shell	Glossy white	Rather reddish white, darkened with bluish tint in upper part
Outside of parietes	Only dark violet longitudinal stripes sharply defined; those in middle and along both sides indistinct or reduced (Fig. 1*a*)	Pale or dark violet longitudinal stripes crossed by the same colored or reddish transverse stripes on the whole area
Inside of parietes	Strongly ribbed up to the sheath; ribs flat on roof and finely denticulate on both sides but not bifurcate distally (Fig. 1*b*)	Slightly ribbed near base; ribs low, with slight denticulation at base which may extend as bifurcate secondary ribs; a few shorter riblets often interseptally (Fig. 1*c*)
Parietal tubes	Numerous (about 16 in rostrum), narrow and square at base (Fig. 1*b*)	Few (about 9 in rostrum), large and rectangular at base (Fig. 1*c*)
Radii	Very broad, flat, with almost level summits, forming an angle of about 100°–110° with the interlocking margin (Fig. 1*a*)	Narrow, slightly sunken, with very oblique summits, forming an angle of about 140° with the interlocking margin
Rostrum	Apex usually incurved	Apex often turned outwards when isolated
Scutum	Depression below adductor ridge deep, oblongly circumscribed (Fig. 2*b*)	Depression below adductor ridge shallow, lengthened along adductor ridge (Fig. 2*d*)
Tergum	Spur very broad, over ⅓ width of the valve, short, either rounded or truncate distally and separated from basi-scutal angle by less than its own width; crests for depressor muscles strongly developed, typically 5 (Fig. 2*a*)	Spur longer than wide, with more or less hatchet-shaped end, separated from basi-scutal angle by its own width which is less than ⅓ that of the valve; crests for depressor muscles not so strong, exceeding 5 in number (Fig. 2*c*)
Labrum	Multidenticulate on each side of a median notch (Fig. 1*e*)	3 teeth, or with a smaller additional one, on each side (Fig. 1*d*)

of this subspecies, compared with the typical *communis*, will help to a certain extent in later identifications.

NATIVE SEA AND HABITAT

From these data of occurrence, it is very likely that the subspecies *hawaiiensis* (= *denticulata*) is not a local variant restricted to such a small area of special environments as the Suez Canal, but nowadays is very widely distributed in circumequatorial tropical and temperate areas in all oceans.

Its native habitat is probably the Hawaiian Islands in the mid-Pacific tropical sea. From this mid-Pacific area it may have spread much earlier and more rapidly in all seas than did the Australasian barnacle, *Elminius modestus* Darwin, in European and South African waters. It is supposed that the first establishment of this Hawaiian barnacle took place from the tropical west Pacific, such as the Philippines and Formosa, lying along the North Equatorial Current, where it is directed westerly, although the most probable means of migration may have been attachment on the hulls of ships.

In these tropical and subtropical areas the

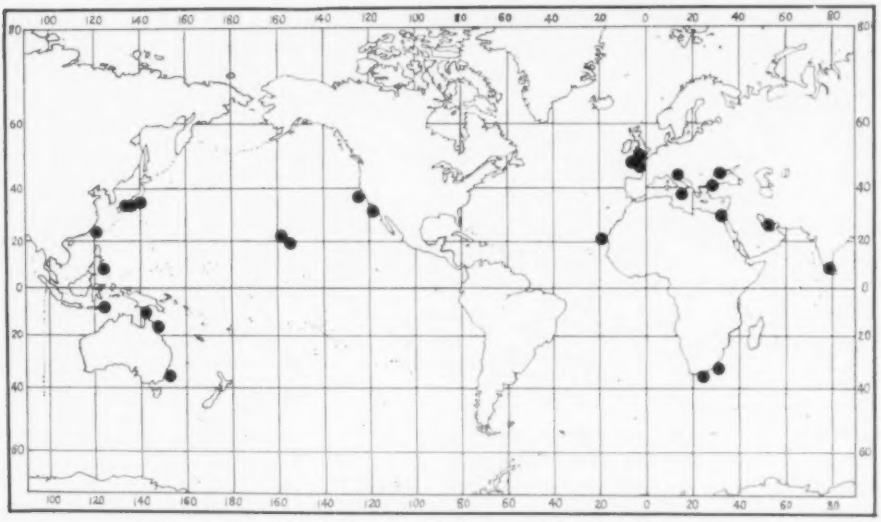

FIG. 3. Geographical distribution of *Balanus amphitrite hawaiiensis* Broch.

barnacles grow abundantly in the intertidal zone of sheltered coasts, usually below the mean sea level; sometimes they occur in clusters on wharf piles, coastal rocks, and mangrove roots on the leeward side but not on seaward reefs with flourishing reef corals.

In the more northern temperate areas, such as the Japanese and Californian coasts, the barnacles are generally restricted to quiet bays or harbors of enclosed water and are usually attached to floats, buoys, ship bottoms, or submerged panels under the low tide level.

They seem to have a tolerance for a wide range of salinities (on the average S 16–30 °/oo), for they are found in the main harbor waters where the salinity is that of normal sea water but may be subject to at least occasional dilution with fresh water. In more estuarine situations they are replaced by *B. amphitrite albicostatus* Pilsbry or by *B. amphitrite krügeri* Nilsson-Cantell. On the other hand, in more saline waters towards the mouth of bays, *B. amphitrite communis* as well as *B. trigonus* Darwin dominate in the subtidal zone. A similar change in barnacle communities has been noted by Day and his collaborators (1956) during their ecological survey of South African estuaries.

From my experience of studies on the fouling organisms of naval ships, I am reminded that *B. amphitrite hawaiiensis* was predominant in Kure port, on the Seto Inland Sea, but was less common in any of the bays facing open seas along the Pacific coast of Japan. There the dominant form was *B. amphitrite communis*.

In this connection it is interesting to find a similar change of habitats in *B. amphitrite denticulata* (= *B. a. hawaiiensis*) established on the Atlantic coasts of France (Bishop *et al.*, 1957). According to them, it is always submerged on the northern coast but is rare or absent on the southwestern coasts of highly estuarine condition.

From these ecological evidences, it seems most appropriate to say that *B. amphitrite hawaiiensis* is a protected-water form rather than a polyhaline form. *B. amphitrite communis*, on the other hand, is a stenohaline subtidal form; and *Elminius modestus* is a more estuarine intertidal form. This last-named barnacle was originally found in a temperate habitat, in European waters, where it had established itself, so that it may extend farther northward than does *B. amphitrite hawaiiensis*.

At any rate, marine animals living in an environment of variable salinity have their reproductive cycle of spawning correlated with the

temperature cycle rather than with salinity. Therefore, as might be expected, there is no particular correlation between successful establishment of fouling organisms and the variable salinity of sea water in the different regions where the barnacle makes a successful settlement.

SUPPLEMENTAL NOTE

After the present paper was submitted, an article by John D. Costlow and C. G. Bookhout, entitled "Larval development of *Balanus amphitrite* var. *denticulata* Broch reared in the laboratory," appeared in the Biological Bulletin, 114(3): 284–295, June, 1958. In this paper they confirmed the fact that *B. amph. denticulata* occurs abundantly as an important fouling organism at Beaufort, North Carolina, on the east coast of North America, and that it is wholly identical with *B. amph. hawaiiensis* in all naupliar stages during metamorphosis. The occurrence of this subspecies there may be supposed also from the illustrations given in Weiss (1948).

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Luminous Organs of the Deep-Sea Squaloid Shark, *Centroscyllium ritteri* Jordan and Fowler

TAMOTSU IWAI[1]

IN THEIR world-wide revision of the squaloid sharks, Bigelow and Schroeder (1957: 47) referred five species to the genus *Centroscyllium*, viz.: *ritteri*, *granulatum*, *fabricii*, *nigrum*, and *ornatum*. Of these, one species only, *C. ritteri* Jordan and Fowler, is recorded from the western Pacific region. Since this species appears to inhabit rather great depths, very little regarding it has been reported. Except for the lower dentition, the taxonomic features of *Centroscyllium* resemble those of *Etmopterus*, which is known to possess a number of minute luminous organs, particularly in a blackish color pattern. The present study was made in order to determine whether *C. ritteri*, like the species of *Etmopterus*, possesses luminous organs.

In regard to the luminous organs of *Etmopterus*, there is sufficient literature to make an accurate review (e.g., Dahlgren and Kepner, 1908: 134; Ohshima, 1911: 1; Schmidt, 1931: 9). But neither detailed accounts of the luminous organs of *C. ritteri* nor a comparison of them with those of species of the genus *Etmopterus* have hitherto been presented, though Burckhardt (1900: 567) briefly dealt with the luminous organs in certain species of *Centroscyllium*. Such a comparison should both extend our knowledge of luminescence in elasmobranch fishes and afford a clearer insight into the nature of their luminous organs.

The author wishes to express sincere appreciation to Prof. K. Matsubara for his cordial guidance and for permission to work on his collection. Thanks are also due to Dr. W. C. Schroeder of the Woods Hole Oceanographic Institution, for a critical review of the manuscript and for furnishing a copy of Burckhardt's paper. The comments and suggestions of Dr. Y. Haneda of the Yokosuka City Museum are gratefully acknowledged.

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MATERIAL AND METHODS

Since *C. ritteri* is relatively rare, only a single specimen measuring 160 mm. from the tip of snout to the origin of upper lobe of caudal fin, and 216 mm. in total length, was available for a dissection. It has been preserved in 10 per cent formalin. The distribution of the luminous organs was first examined by means of a binocular microscope. Then the skin was removed for the microscopic preparations. Sections were made by the usual paraffin method at a standard thickness of 10 μ. The staining methods used were Mayer's hemalum-eosin and Mallory's triple stains.

In order to make a comparison of the luminous organs an embryo of *Etmopterus lucifer* Jordan and Snyder measuring 135 mm. in total length was also sectioned.

OBSERVATIONS AND DESCRIPTIONS

Distribution of the Luminous Organs

The luminous organs of *C. ritteri* are widely distributed over the body surface and some of the fins, though gradation is not uniform throughout the body. The organs are so numerous that their total number is difficult to estimate. Each organ is very small, 0.11–0.15 mm. in diameter, and is provided with a pigment sheath. In addition, these sink within the epidermis. Therefore, it is scarcely possible to observe the organs with the naked eye. However, they can be seen as small black spots under a low magnification.

In general, the densely distributed areas of luminous organs agree well with the jet-black color pattern marked on the body. The ground color of the head and body preserved in formalin is chocolate brown, but the tip and ventral surface of head are black, as is the belly. The first and second dorsal fins and the pectoral fin are edged with a white band. There are distinct black markings on the ventral surface of the

upper eyelid, the base of the pectoral fin, the flank, and the ventroposterior corner of the caudal peduncle. These blackish areas are equipped with a greater number of luminous organs than are the other portions of the body. The most concentrated area of organs is the flank, which is dotted with black pigments (Fig. 1), the number of organs being 11–14 per square mm. On the other hand, the luminous organs are most sparse on the dorsal region of the body, excluding the head. On this area few luminous organs could be recognized.

Of particular interest is the presence of luminous organs studded on the ventral surface of the upper eyelid (Fig. 2). They are most conspicuous on both the anterior and posterior portions of the upper eyelid, but are poorly developed or absent at the central portion immediately above the eyeball.

Histological Features of the Luminous Organs

The epidermis of *C. ritteri*, in which the luminous organs are embedded, is composed of a stratified squamous epithelium with some mucous cells. This layer is lined with the stratum of dermis which consists of fibroelastic tissues (Fig. 3). Throughout the luminous area there extends a thin layer of pigment cells between the dermis and the epidermis, and the luminous organs are usually set on this pigment layer. On the scaled area the organs are found to be scattered among the placoid scales. Most of the luminous organs are obliquely situated and slightly inserted in the distal portion of the dermis.

Each luminous organ is a hemispherical cup in shape, and is composed of four main elements, (1) photogenic cells, (2) an irislike structure of pigment cells, (3) lens cells, and (4) a pigment sheath covering the organ.

The photogenic cells, approximately 7–12 in number, occupy the bottom of the organ. These cells are of a glandular type with an eosinophil secretion in their distal portion. Photogenesis seems to be intracellular. The lower half of a mass of photogenic cells is covered directly with the pigment sheath without a reflectorlike structure (Fig. 3).

Along the peripheral border of the mass of photogenic cells, there is a crowding of the pigment cells (Fig. 3). These are arranged in a circle and send out dendritic inward projections covering the cup. They apparently are capable of controlling themselves in the area which intercepts the photogenic body. This structure, therefore, may serve as an iris to regulate the amount of the light emitted from the photogenic cells. The arrangement of pigment cells of this structure resembles that of *Etmopterus frontimaculatus* rather than *E. lucifer*, described by Ohshima (1911: 4). The irislike structure of the latter species is more developed, that is, the pigment cells extend further toward the lens cells (Fig. 4).

Each luminous organ bears two or three lens cells lying above the cup. These cells are peculiar in containing a large amount of homogeneous concretion stained with orange G in cytoplasm, though some are vacuolated. This fine structure perhaps acts as a lens to concentrate the light emitted from the photogenic body. The nucleus, ovoid in shape, lies near the base of the cells. Because of the lack of young material, it was

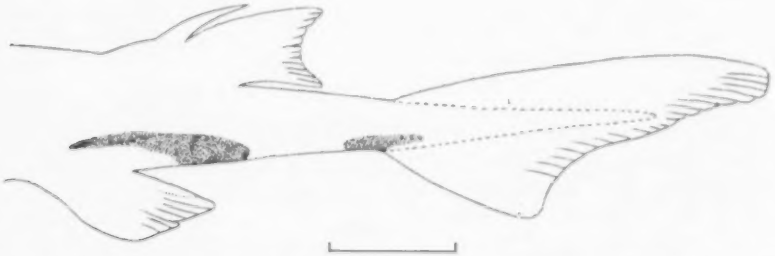

FIG. 1. Lateral aspect of posterior part of *Centroscyllium ritteri*, showing black markings on the flank and caudal peduncle in which luminous organs are densely distributed. Scale bar indicates 10 mm.

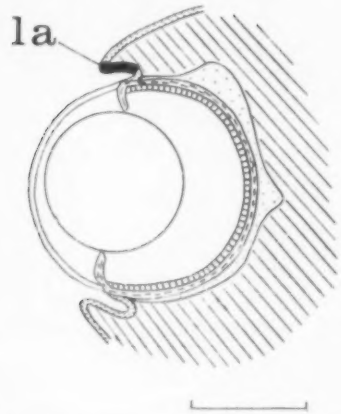

FIG. 2. Diagrammatic aspect of cross section through the eye, showing the supraorbital luminous area (1a). Scale bar indicates 5 mm.

impossible to trace a sequence of development of the lens cells. The staining reaction of the lens cells in this species is quite dull as compared with that of *E. lucifer* (cf. Figs. 3, 4). This may be due to a poor condition of fixation.

The proximal border of the luminous organ is lined with the cup-shaped pigment sheath (Fig. 3), which may prevent the diffusion of light to the lining stratum. It continues to the iris at the distal end.

There is no reflectorlike structure at the base of the photogenic body, whereas highly developed luminous organs of teleostean fishes are usually provided with a well-developed reflector.

The histological examinations mentioned above show that the luminous organs of *C. ritteri* are not as well developed as those of *E. lucifer*, either in number or in structure. But as far as the structural evidence is concerned, it is not unreasonable to assume that these organs may be functional.

DISCUSSION

In the absence of living material, there is doubt as to whether or not the luminous organ of this shark is functional. Ohshima (1911: 7) and Schmidt (1931: 9), both working with living *Etmopterus frontimaculatus*, observed that feeble luminosity appears throughout the ventral surface and that the light is not produced spontaneously but is emitted regularly by mechanical stimulation. The fact that the location and structure of the organs of *C. ritteri* are virtually the same as those of *Etmopterus* may imply that the present deep-sea shark is luminous. In his work on the luminous organs of elasmobranch fishes, Burckhardt (1900: 567–568) found luminous organs in both *Centroscyllium granulatum* and *C. fabricii*. Bigelow and Schroeder (1957: 38) also suggested the possibility of luminescence with thickenings of the black skin in some species of *Centroscyllium*. These data would lead one to suppose that all the members of *Centroscyllium* possess luminous organs, as is the case with the genus *Etmopterus*.

In several groups of fishes the characters of the luminous organs have been adequately discussed and appear to offer good evidence for separating the species. Haneda (1950: 216) and Matsubara (1953: 21) recognized two distinct species of the genus *Acropoma* based chiefly upon the form of the luminous organ, though the latter author added further features which enable us to distinguish the species. Iwai and Asano (1958: 8), upon studying the structure of the luminous organs as well as other

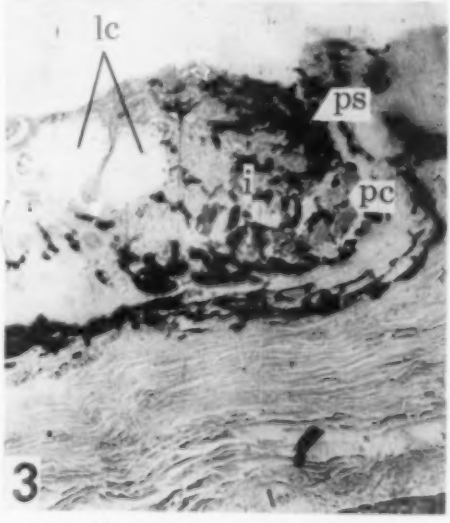

FIG. 3. Transverse section through a luminous organ on the flank of *C. ritteri*. (× *ca.* 350). i, Iris; lc, lens cell; pc, photogenic cell; ps, pigment sheath.

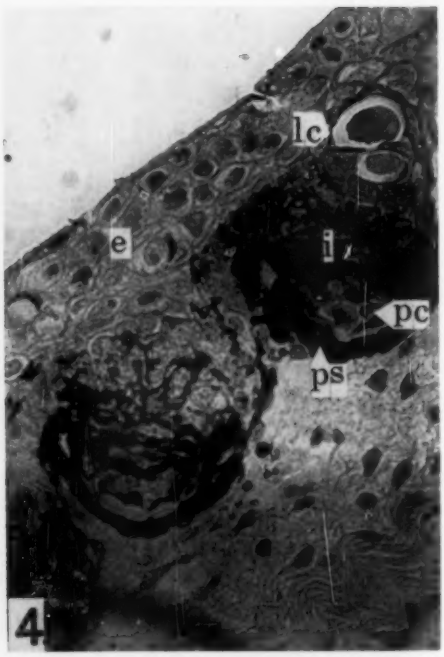

FIG. 4. Photomicrograph of section showing two luminous organs on the flank of *E. lucifer*. (× *ca.* 350). ed, Epidermis; i, iris; lc, lens cell; pc, photogenic cell; ps, pigment sheath.

characteristics, concluded that *Apogon marginatus* should be a synonym of *A. ellioti*. In their key to the species of *Etmopterus*, Bigelow and Schroeder (1957: 61) utilized the black markings on the flank which include the heavily dotted pigment cells of the luminous organs. Judging from the results of the present study it seems likely that the distribution of luminous organs, especially those on the flank and caudal peduncle which form peculiar markings, serves as one of the specific characters of the genus *Centroscyllium*.

Attention should be called to the curious placement of luminous organs on the ventral surface of the upper eyelid. The situation of these organs is similar to the series *Li* of *Chauliodus sloani* Schneider described by Tchernavin (1953: 68). The latter consists of 4–6 cup-shaped organs situated within the fold of skin above the eye. The role of these organs is unknown, but Tchernavin (1953: 68) suggested that such orbital photophores serve to illuminate approaching prey or to excite the eye.

SUMMARY

1. *Centroscyllium ritteri* Jordan and Fowler, like the other species of *Centroscyllium* or *Etmopterus*, is provided with a number of minute luminous organs on the body surface.

2. The densely distributed areas of luminous organs agree well with the jet-black color pattern marked on the body, especially those on the ventral surface of the upper eyelid, belly, and flank.

3. Each luminous organ is composed of the photogenic cells, an irislike structure of pigment cells, the lens cells, and a pigment sheath.

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Analysis of Sea Bird Distribution in the Northwest Pacific Ocean

NAGAHISA KURODA[1]

THIS PAPER is based on data obtained by the author on board the fur seal research ship, "Geizan Maru," No. 8 (capacity, 78 tons), of the Japanese Fisheries Bureau, between June 4 and July 14, 1954, on a trip from Japan to the west Bering Sea. This paper presents the relative abundance of sea birds by divisions of sea zones, and discusses their correlation with air and water temperatures. Specific records on birds and sea mammals have been reported in other places (Kuroda, 1955, 1956) and a diary of the cruise has been prepared (in MS).

METHOD

All of the sea birds observed were recorded, together with pertinent data upon the time, air and water temperatures (these were regularly measured every hour by the crew), and the location in longitude and latitude. When flocks of birds were seen, their number was estimated. The author was the observer for an average of seven hours a day, with two or three rest periods. The records were arranged in a table under each observation time. The numbers of individuals observed per day and per hour were calculated (Table 1). Specimens of almost all of the species recorded were obtained (Kuroda, 1955).

GENERAL REMARKS

Although it was the breeding season, observations were concerned chiefly with nonbreeding populations of sea birds, since the ship took a pelagic course.

The density of sea birds can be given by linear and dimensional estimates. The linear estimate may be either per unit of time or per unit distance of travel. In this paper, the number of birds observed per hour, at a ship's speed of seven miles per hour, was used for various analyses. For the absolute population density of sea birds, the following formula, which was developed in research upon the fur seal (Austin & Wilke, 1950: 35; also in 1954) might be applied:

$$\text{Number of birds per square mile} = \frac{\text{Total number of birds observed}}{\text{Distance passed during observation (in miles)} \times 0.114}$$

The fur seal frequently rests on the water, exposing only small parts of its head and flippers. The figure 0.114 mile is the distance to each side of the ship at which the seal can be visually detected when in this position. To collect adequate data for a certain sea area, several ships should work, as in the fur seal census, or a single ship should take a zigzag or irregular course to cover a greater part of the sea area by that "sight range belt." In our research, the latter type of course was taken in the northern sea and dimensional bird density was calculated tentatively, applying the above formula for subdivisions of this sea zone (Table 2). But the significance of the sight range of 0.114 mile in the study of birds needs future study, and, in actuality, all of the identifiable species of birds were recorded, irrespective of distance. It has been our experience, however, in many cruises off Japan, that floating sea birds were often identified at about the same range as the fur seals were detected, although a closer range was necessary to identify such similar species as *Synthliboramphus antiquus* and *S. wumizusume*, because binoculars are not usable, owing to vibration on a small research ship. On the other hand, flying birds, especially when in flocks, can be seen and identified at much greater distances, but some closely similar species, such as *Puffinus tenuirostris* and *P. griseus*, must often be identified at a closer range. Moreover, weather, direction of sunlight, and wave conditions influence very much the visibility and the success of the observer's identifications.

[1] Yamashina Museum of Birds, 49 Nanpeidai-machi, Shibuya, Tokyo, Japan. Manuscript received March 5, 1958.

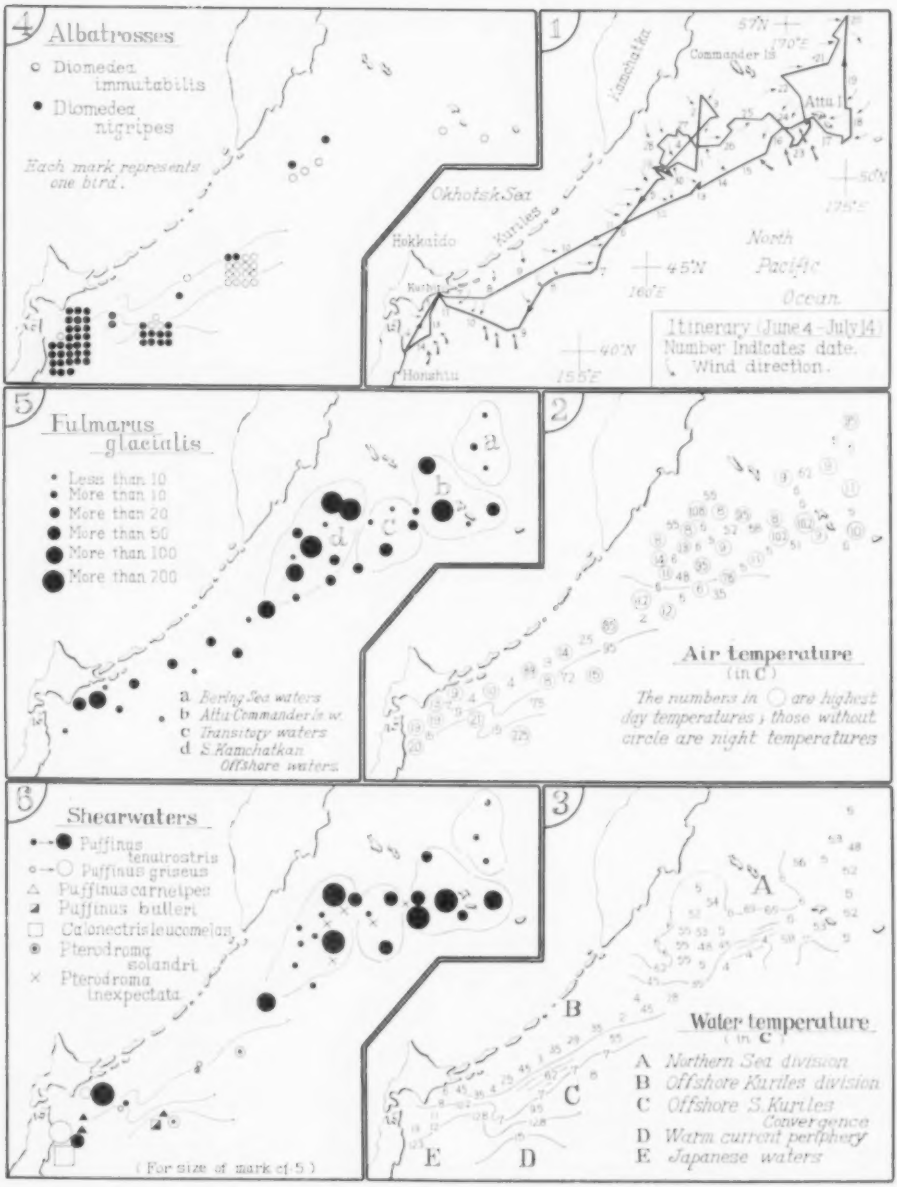


FIG. 1*a*. Maps showing the oceanographic conditions, sea divisions, and distribution of the birds observed and collected. Bird abundance is based on daily counts of individuals.

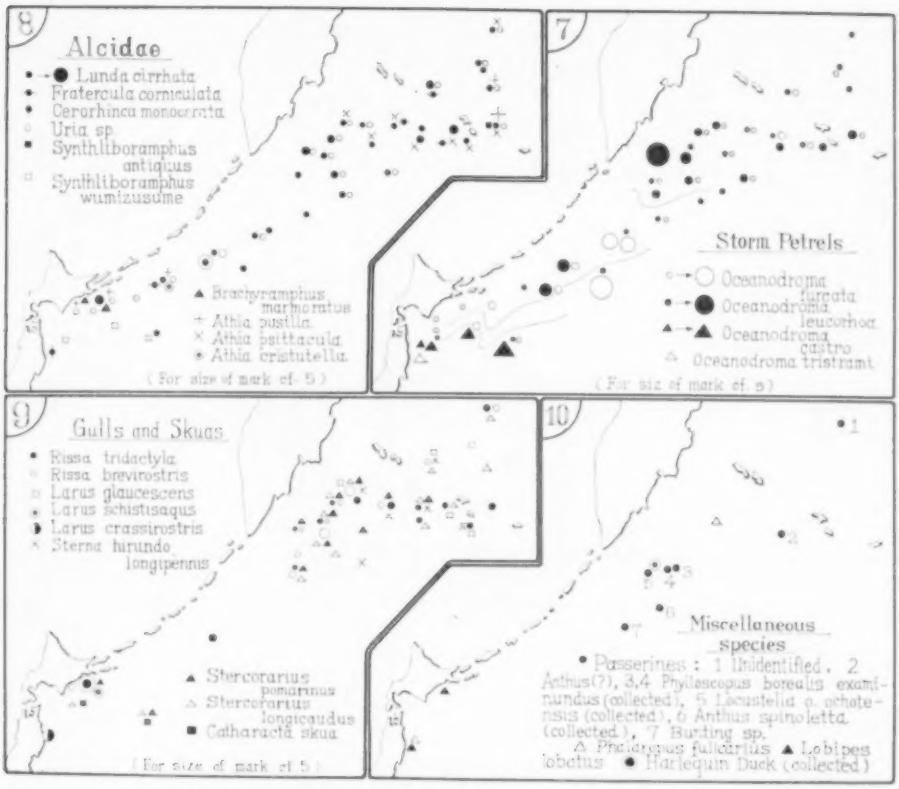


FIG. 1*b*. Maps showing the distribution of the birds observed and collected.

For comparative study of sea bird distribution, specific relative abundance within a sea zone and zonal relative abundance inclusive of all species occurring in the zone, will be considered. The distribution of sea birds is subject to three general sources of variation: zoogeographic (endemism), ecological (food and temperature dependent), and seasonal (physiological cycle and migration). These factors influence the occurrence of various species and the relative abundance of birds in different sea zones.

Each species has its range of physiological tolerance to temperature, both in air and in water, although this is less strict in some species and varies seasonally to some extent. Furthermore, a few individuals may stray out of this range, and long-distance migrants of cold currents cross the tropical seas. Within a preferred temperature sea zone, the food supply and interspecific relation in some cases determine the local relative abundance of sea birds and form a basis for subdividing the sea zone.

The *specific relative abundance* of sea birds within a sea zone was estimated by the "specific lowest density" per hour (of Elton, 1953: 51), which is:

$$\frac{\Sigma \text{ Number of birds observed per hour}}{\text{Total number of observation days}}$$

In this calculation of lowest density are included the days on which the species has not been recorded. Therefore, it is lower than the

TABLE 1

AN EXAMPLE OF THE DAILY RECORDS AND NOTES FROM THE AUTHOR'S OBSERVATION DIARY

OBSERVATION TIME	6:00–7:30 a.m.	11:00–15:00	16:00–18:00	Total time: 7:30 hours	Number observed per hour (7 miles)
AIR TEMPERATURE (°C.)	7–9	9–11	7.5–6	Distance: 52 miles	
WATER TEMPERATURE (°C.)	4.2–4.3	4	4		
				TOTAL	
Fulmarus glacialis	3	51	10 (white 1)	64 (white 1)	8.76
Oceanodroma furcata	3	3	7	13	1.78
O. leucorhoa	—	—	1	1	0.13
Puffinus tenuirostris	—	40	11	51	6.98
Lunda cirrhata	3	1	—	4	0.54
Total	9	95	29	133	18.19
Fur Seal	1	—	—	1	—
Phocaenoides dallii	—	about 5	—	5	—

Date: June 15. Cloudy, occasional fine rain. Air pressure: 1008 mb.

Wind: E–ESE (1–0), dead calm. 270–200 miles WSW of Attu Is.

Note: Passed 50° N. latitude, heading toward Attu. Fulmar increased (white one seen at 167° 28′ E., 50° 52′ N.) and a flock of *P. tenuirostris* occurred, flying to E–NE, obliquely against winds. Water temperature changed from previous 3° C. to 4° C., with demarcating line NE–SW.

"economic density" of Elton, which is the density of a species when it occurs, calculated by this formula:

$$\frac{\Sigma \text{ Number of birds observed per hour}}{\text{Number of days the species was observed}}$$

Then, the species' abundance (general or localized distribution) is suggested by the "occurrence rate," which is:

$$\frac{\text{Number of days the species was observed}}{\text{Total number of observation days}}$$

Therefore, from these formulae, the following relation exists between the lowest and economic densities:

$$\text{lowest density} = \text{economic density} \times \text{occurrence rate}$$

The *areal relative abundance* of sea birds was compared by the areal "lowest density" per hour, which is:

$$\frac{\Sigma \text{ Number of birds of all the species observed per hour}}{\text{Number of observation days}}$$

and the "abundance rate of species" was calculated by:

$$\frac{\text{Mean number of species which was observed per day}}{\text{Total number of species observed}}$$

The *distributional pattern* of species depends upon their habits. If systematic areal census of the sea birds could be made, they would show interesting distributional patterns (Odum, 1954: 154; Torii, 1952) by species and by sea zones. Flocking species, such as shearwaters, concentrate in a clustered pattern where food is abundant; the phalaropes, which feed on plankton, show a patchy pattern of small groups; while the tufted puffins usually occur at random singly or in pairs. Possibly in the case of the puffins, a sparse food supply is enough to sustain their solitary life on the ocean.

TABLE 2

POPULATION DENSITIES OF SEA BIRDS IN THE SUBDIVISIONS OF THE "NORTHERN SEA DIVISIONS"

SEA AREAS	NUMBER OF BIRDS OBSERVED PER DAY	NUMBER OF SPECIES OBSERVED	NUMBER OF BIRDS PER HOUR (AT 7 MILES)	NUMBER OF BIRDS PER SQUARE MILE
W. Bering Sea	38	8	7	7.42
Attu–Commander Is.	307	10	40	49.11
In Transit	112	8	17	21.19
Offshore S. Kamchatka	280	9	50	59.81

Data on 10 chief species of birds recorded in the Northern Sea Division are analyzed in Table 3 and Figure 2. The mean economic density roughly represents the general specific density, but by inclusion of some concentrated and irregular densities, the species' most frequent density, the mode, is obscured (Table 3). In the Tubinares (*Fulmarus glacialis, Puffinus tenuirostris*, and *Oceanodroma furcata*) the range of observed densities is very wide, because they usually occurred sparsely during the day and often formed a large feeding flock, especially in the early morning. (*O. leucorhoa* was an exception, but its chief concentration was outside of this sea division.) These two patterns of distribution were well marked, as shown in Figure 2A; the most frequent densities of usual sparse distribution (the mode) were 1–3 birds per hour, while the concentrated densities (the "highest density" of Elton) were as high as 30–70 birds per hour. In other sea birds, such as alcids and gulls, such a "highest density" concentration was not found. But their numbers increased (Fig. 2B; June 23, July 2–5, etc.) when they were found among a mixed community, with porpoises and perhaps some fishes under the water feeding upon euphausids. The dominant birds were *Fulmarus glacialis* and/or *P. tenuirostris*. One such fulmar-dominated concentration was found close to a mother ship (6,000 tons) of the Japanese salmon fishery, on July 4–5.

Puffinus tenuirostris birds are migrants from the southern hemisphere and *Fulmarus* was represented perhaps chiefly by a nonbreeding population. Some breeding adults (a bird with large ova was collected), as well as some molting young of *Lunda cirrhata*, were found as far as 200 miles offshore, and they were distributed rather uniformly, with a density of 1–3 birds per hour. But a species of *Uria* seemed to be less pelagic in distribution and only a sparse peripheral population was encountered, since the usual densities were 0.1–0.2 birds per hour. *Rissa* spp. are gregarious pelagic gulls, but apparently only some nonbreeding birds were found, inasmuch as their distributional pattern was sparse and irregular.

DIVISIONS OF SEA ZONES

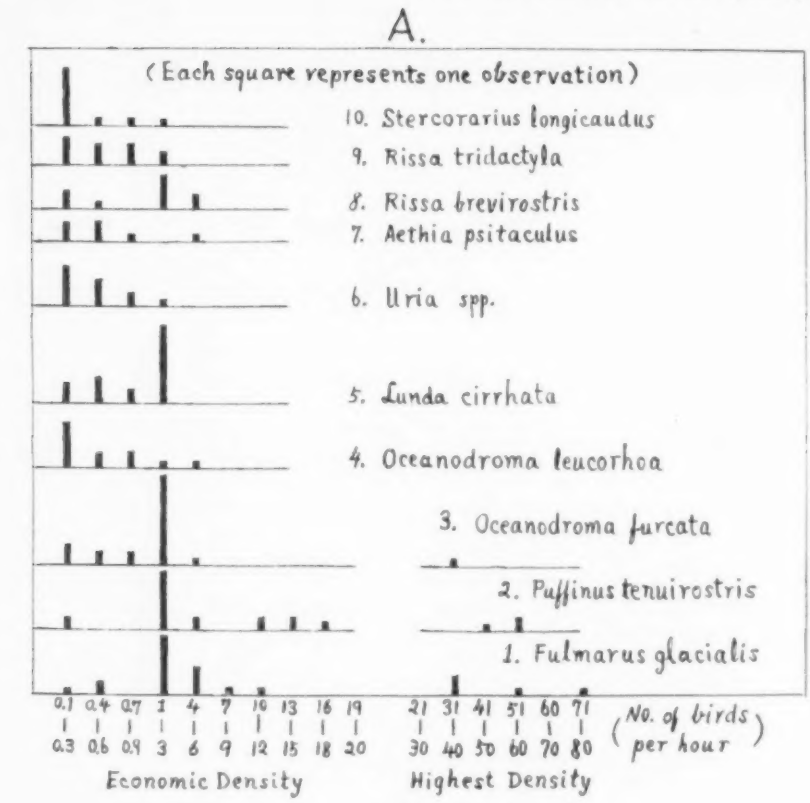
The cruise track of the "Geizan," No. 8, and the sea divisions traversed, are shown in Figure 1. Oceanographic conditions (Kuroda, 1955) and sea bird distribution in each division and subdivision are briefly given below (see also Figs. 1, 3, and Table 4).

A. *Cold Current Sea Surface*

From the northern seas the cold current stretches along the Kuriles (at least to 100 miles offshore) south to Hokkaido. The dominant species of sea bird was *Fulmarus glacialis*. Other generally distributed species were: *Puffinus tenuirostris* (rare along the Kuriles), *Lunda cirrhata, Oceanodroma furcata* (rare off the central Kuriles and southward), and *O. leucorhoa* (rare in the northern seas).

1. Northern sea division

North of about 50° N. latitude. The air and water temperatures were most often 5°–6° C. and 8°–10° C. respectively. At night water temperatures often fell to 5° C. Zoogeographic species characteristically not found southward were: *Rissa brevirostris* (see its


A.
(Each square represents one observation)
10. Stercorarius longicaudus
9. Rissa tridactyla
8. Rissa brevirostris
7. Aethia psitaculus
6. Uria spp.
5. Lunda cirrhata
4. Oceanodroma leucorhoa
3. Oceanodroma furcata
2. Puffinus tenuirostris
1. Fulmarus glacialis
0.1 0.4 0.7 1 4 7 10 13 16 19
0.3 0.6 0.9 3 6 9 12 15 18 20
21 31 41 51 60 71
30 40 50 60 70 80
(No. of birds per hour)
Economic Density
Highest Density
B.
10.
9.
8.
7.
6.
5.
4.
3.
2.
1.
rest
12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 1 2 3 4 5
June
July
: 0.3 birds per hour
: 3 birds per hour
: More than 30
: More than 50
: More than 70

distribution with that of *R. tridactyla*, in map), *Larus glaucescens*, and *Aethia psittaculus*. Among migrants, northern breeding species such as Nordmann's Tern, skuas, etc., were found mainly in this division in late June, and *Pterodroma inexpectata* represented a southern hemisphere migrant. Further subdivisions with different sea bird densities were as follows:

a. Bering Sea waters: Bird density was very low but *Rissa brevirostris* was relatively common. Birds of this species contained a large amount of body fat, but one collected specimen of two *Rissa tridactyla* encountered was entirely devoid of fat. Possibly both were stragglers.

b. Attu–Commander Is. waters: Towards the Commander Is., the fulmars increased, showing clustered distribution around discarded viscera of whales. Apparently food supply was abundant near the islands and bird density was high. A big mixed flock of *Fulmarus glacialis* and *Puffinus tenuirostris* (and of other sea birds and the porpoise, *Phocaenoides dallii*) was devouring euphausids at dawn, June 23, west of Attu, where meeting lines of currents occurred and some southerly summer winds were blowing. East of Agattu, where there was a strong local water current, alcids such as *Aethia psittaculus* and *A. pusilla* were abundant. *Rissa tridactyla* was not uncommon but no *R. brevirostris* was seen.

c. Transitory waters: A generally pelagic zone with medium bird density. Main species were: *Fulmarus glacialis*, *P. tenuirostris*, *O. furcata*, and *O. leucorhoa*, as well as occasional *Pterodroma inexpectata*.

d. S. Kamchatkan offshore waters: Bird density, especially of *Fulmarus* and *P. tenuirostris*, was again high and a marked concentration of *O. furcata* was found. *Lunda* and *Uria* (mostly *U. aalge*) as well as skuas (*Stercorarius pomarinus* and *S. longicaudus*) became common, while *R. brevirostris* (total seen 113) outnumbered *R. tridactyla* (total seen 36), June 25–July 5.

2. Offshore Kuriles division

A stretch of sea surface influenced by cold winds and waters of the Okhotsk Sea. The bird density was sparse, the dominant species being *Fulmarus* as usual. *O. leucorhoa* outnumbered *O. furcata*, which decreased towards the south. *Lunda* was found scattered and *R. tridactyla* occurred, but *R. brevirostris* was not observed. *Aethia cristatella* was found extremely localized off Shinshiru Is.

B. *Offshore Kuriles Convergence (180–200 miles offshore)*

Outside the Kuriles cold current a zone of convergence was found between the cold current and the periphery of the warm current, and some demarcating lines were noted. A change in relative abundance was noted, *O. leucorhoa* becoming the dominant species, and *O. furcata* and *Fulmarus* as well as *Lunda* decreased. *Diomedea immutabilis* seemed to be most suited to this intermediate temperature zone, while warmer adapted species, such as *D. nigripes*, and *Pterodroma solandri* (first recorded in this zone) began to appear.

C. *Offshore Warm Current Sea Surface*

At a point just north of 41° N., 240 miles E.S.E. of Kushiro, Hokkaido, the periphery of the warm current was reached; there the sky cleared up and the sea was very blue and calm with gentle southern breezes (air 22° C. and water 15° C.). Such fish as the swordfish, sharks, and sunfish, which characterize the warm current, occurred there, and *Phocaenoides dallii* was replaced by *Lagenorhynchus obliquidens*, while the sperm whale was observed in family groups. A radical change in bird species was noted. No species occurred in large flocks, which, perhaps, was evidence of the scarcity of plankton, the basic food supply. In this zone *D. immutabilis* was replaced by *D. nigripes* and *O. leucorhoa* by *O. castro*. Such southern hemis-

FIG. 2. Distributional patterns of sample species in the Northern Sea division.

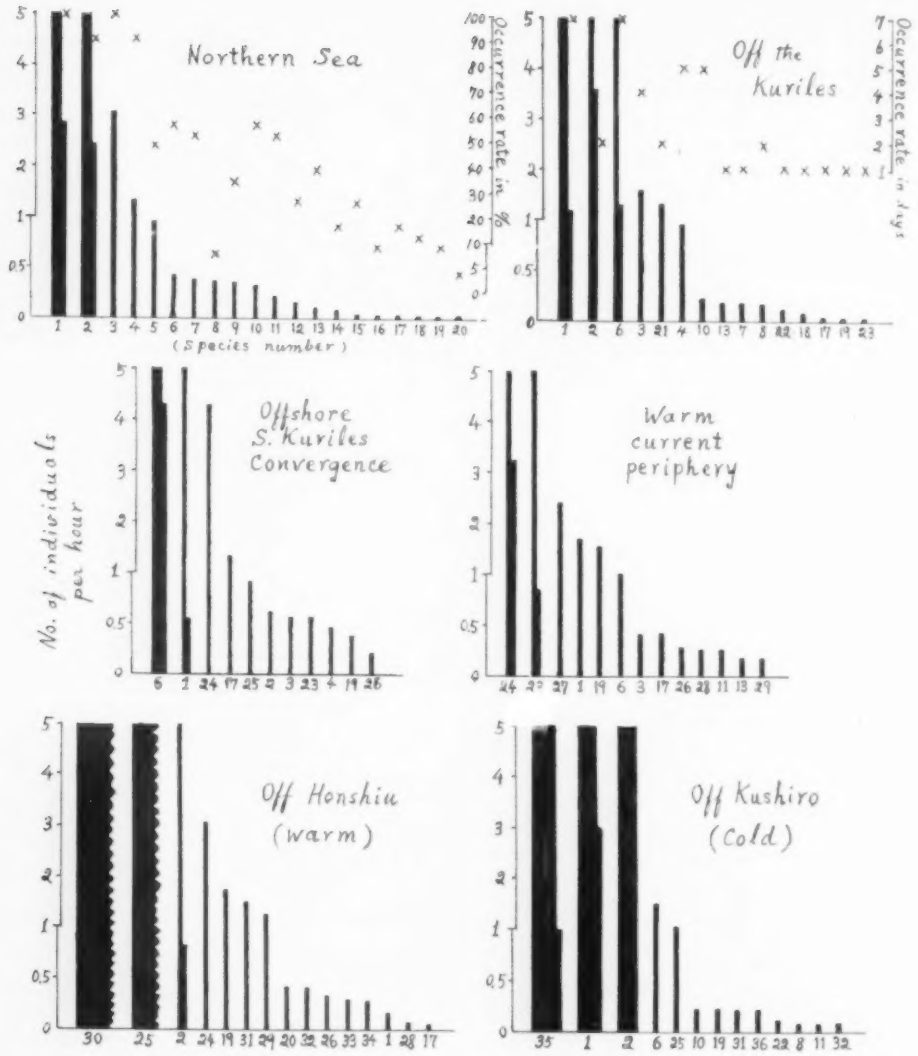


FIG. 3. Relative abundance (number of individuals per hour) of all of the species of sea birds recorded in each sea division. Species numbers indicate: 1. *Fulmarus glacialis*, 2. *Puffinus tenuirostris*, 3. *Oceanodroma furcata*, 4. *Lunda cirrhata*, 5. *Rissa brevirostris*, 6. *Oceanodroma leucorhoa*, 7. *Rissa tridactyla*, 8. *Aethia pusilla*, 9. *Aethia psittaculus*, 10. *Uria* sp., 11. *Stercorarius longicaudus*, 12. *Pterodroma inexpectata*, 13. *Stercorarius pomarinus*, 14. *Larus glaucescens*, 15. *Sterna hirundo longipennis*, 16. *Synthliboramphus antiquus*, 17. *Diomedea immutabilis*, 18. *Fratercula corniculata*, 19. *Diomedea nigripes*, 20. *Phalaropus fulicarius*, 21. *Aethia cristatella*, 22. *Brachyramphus marmoratus*, 23. *Pterodroma solandri*, 24. *Oceanodroma castro*, 25. *Puffinus griseus*, 26. *Synthliboramphus wumizusume*, 27. *Puffinus bulleri*, 28. *Catharacta skua*, 29. *Puffinus carneipes*, 30. *Calonectris leucomelas*, 31. *Larus crassirostris*, 32. *Lobipes lobatus*, 33. *Cerorhinca monocerata*, 34. *Oceanodroma tristrami*, 35. *Larus schistisagus*, 36. *Larus canus*.

TABLE 3

ANALYSIS OF POPULATION DENSITIES AND PATTERNS OF CHIEF SPECIES OF SEA BIRDS IN THE "NORTHERN SEA DIVISIONS," 12 JUNE–5 JULY 1954

SPECIES OF BIRDS	ECONOMIC DENSITY			NUMBER OF INDIVIDUALS PER HOUR		OCCURRENCE RATE‡	LOWEST DENSITY
	Variation	Mean	S.D. (6)	Mode†	Mean		
Fulmarus glacialis	0.3–12.2 *32.9–76.2(5)	12.86	19.0	1.4–3.2	2.43	1.00	12.86
Puffinus tenuirostris	0.3–17.8 *46.6–60.8(3)	13.69	18.0	1.2–3.7	2.19	0.91	12.45
Oceanodroma furcata	0.1– 4.6 *40.0	3.07	8.0	1.1–2.3	1.58	1.00	3.07
O. leucorhoa	0.1– 4.0	0.73	0.9	0.1–0.4	0.28	0.56	0.41
Lunda cirrhata	0.1– 3.7	1.46	1.0	1.1–3.7	2.18	0.91	1.33
Uria spp.	0.1– 2.1	0.55	0.6	0.1–0.2	0.20	0.56	0.31
Aethia psittaculus	0.1– 4.8	1.00	1.5	0.1–0.6	0.43	0.34	0.34
Rissa brevirostris	0.1– 6.5	1.92	1.9	0.2–2.7	1.90	0.47	0.90
R. tridactyla	0.1– 2.0	0.73	0.6	0.1–0.2	0.13	0.52	0.38
Stercorarius longicaudus	0.1– 1.8	0.39	0.4	0.1–0.3	0.16	0.52	0.20

* Indicates concentrated or "highest" density: 5 cases in *Fulmarus*, 3 in *P. tenuirostris*, and 1 in *O. furcata*. These are included in the means.

† The mode indicates most frequent densities, exclusive of unusual or "highest" densities.

‡ Occurrence rate is the ratio between the number of days the species occurred and the total of 23 observation days. The lowest density is the mean economic density × the occurrence rate.

phere migrants as *Pterodroma solandri* and *Puffinus bulleri* (first recorded) were common, and a few *Puffinus carneipes* and *Catharacta skua* occurred, while *Synthliboramphus wumizusume* reached there from its Japanese breeding waters.

D. *Japanese Waters*

1. Warm waters off Honshu

The oceanic conditions are similar to area C above, but the water temperature was lower (12°–13° C.), and cold and warm currents were distinguished at about the latitude of Cape Erimo, Hokkaido. *D. nigripes* became common south of that latitude and *P. carneipes*, *O. castro*, and *Catharacta skua* occurred, while a few *Fulmarus* and a single straggler of *O. furcata* were seen south to 143° 42′ E., 41° 23′ N. Two *Fulmarus* were sighted as far south as Iwate, Honshu. The coastal waters of Sanriku (N. Honshu), where currents meet and which are rich in food supply, were the main summering grounds of *Puffinus griseus*. Nearer to the coast, some 2,000 *Calonectris leucomelas* were observed off Yamada Bay, apparently over a shoal of sardine; *P. griseus*, with a weaker bill, prefers to feed upon euphausids. These two species were responsible for the very high population density of this coastal zone.

2. Cold waters off Kushiro, Hokkaido

In this southern limit subdivision of the cold northern waters, *Fulmarus* and *P. tenuirostris* were again numerous and *Larus schistisagus* and *Brachyramphus marmoratus* occurred in coastal waters.

CORRELATION WITH FOOD SUPPLY

The abundance of plankton, a basic food supply of sea birds, is correlated with local upwellings of the sea which are caused by sea bottom conditions (especially near islands), and currents as well as winds. A special study of

DATE	SEA AREA	PLANKTON	POLLACK ANGLED	NO. OF BIRDS OBSERVED
June 17	Near Agattu	Very scarce (collected)	15	61
June 18	Agattu-Kiska Strait	—	49	285
June 22	60 m. E. of Commander Is.	Abundant (collected)	Scores	190
June 23	W. of Attu Is.	Abundant (euphausids)	—	659 (A big flock)
June 26	200 m. S. of Commander Is.	Scarce (collected)	—	77

plankton was not made, although in some collections made for the Fisheries Bureau, *Sagitta* species were very abundant locally, but the following may show some relationship with bird density.

Pollack were caught for a short time after sunset by 4–5 crew members, and it is indicated in the data above that a correlation exists among abundance of plankton, pollack, and sea birds. In the tropical Pacific, Thompson (1951) found a parallel increase of jellyfish and the black-footed albatross toward cooler waters, and from his observation he derived a "Jellyfish Index." In the above case, the "Pollack Index," the number angled per unit of time by the same persons, might serve as an index of productivity in northern seas.

TEMPERATURE PREFERENCE IN SOME SEA BIRDS

As mentioned above, the sea birds are either cold or warm adapted, therefore temperature dependent in distribution. This is best shown by the Tubinares, as briefly described below (see Fig. 4).

THE ALBATROSSES: Of the two species, *Diomedea immutabilis* is less warm adapted. It was commonest in the convergent sea surface, and *D. nigripes* distinctly preferred the warm current zone. But even the latter species is not a tropical bird. Thompson (1951) reports an increase in number as the water temperature decreased from 27.7° C. to 14.4° C. in the eastern Pacific. During its winter breeding season, the air and water temperatures around the subtropical islands, Torishima or Bonin Is., are both below 20° C. The temperatures markedly increase during the summer when *D. nigripes* moves north to cooler waters. This cool adaptation could explain their winter reproductive cycle, which is unusual for the northern hemisphere (Kuroda, MS). From my observation, the temperature preference of the two species is suggested below.

	D. immutabilis	*D. nigripes*
Air Temperature (°C.)		
Range	6.2–22.5	7.0–22.5
Preferred	13–15	17–22.5
Water Temperature (°C.)		
Range	5–15.5	5–16
Preferred	7–8	10–16

THE STORM PETRELS: Both *Oceanodroma furcata* and *O. leucorhoa* are cold adapted species, although the latter shows wider temperature adaptation as it migrates in winter to tropical waters. Zoogeographically their main distribution ranges were segregated north and south, although they overlapped. A distinct concentration of *O. furcata* was found in the north in waters east of south Kamchatka (air temperature, 7–8° C.; water temperature, 5.6–7.3° C.), while concentrations of *O. leucorhoa* occurred in the Offshore Kuriles Convergence (air 13–15° C., water 6.6–8° C.), where *furcata* decreased. But just north of this concentration, *O. leucorhoa* also showed a clustered distribution, both on June 11 and July 6, within the cold Kuriles current (air 3.5–4 and 9.2–11° C., water 2.3–3 and 5° C.). In this case, too, the

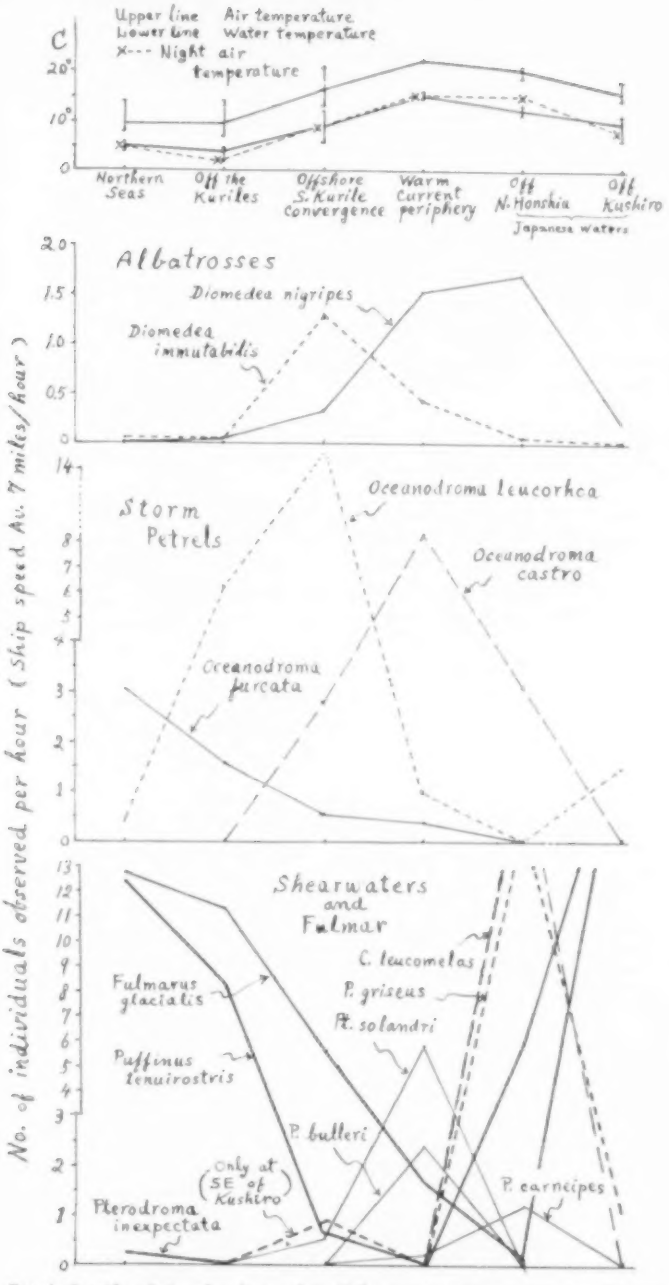


FIG. 4. Specific relative abundance of the Tubinares in different temperature zones.

TABLE 4

POPULATION DENSITIES OF SEA BIRDS IN THE SEA DIVISIONS INVESTIGATED

	COLD CURRENT		OFF-SHORE SOUTH KURILES CONVERGENCE	WARM CURRENT PERIPHERY	JAPANESE WATERS		TOTAL OR AVERAGE
	Northern Sea	Off the Kuriles			Off Honshu (warm)	Off Kushiro (cold)	
Number of days of navigation	23	7	2	1	2.5	2.5	37
Total number of birds observed	4136	761	309	160	2699	983	9048
Number of birds observed per day (average)	31–604 179.8	39–281 108.7	154.5	160.0	1075.6	392.2	345.1
Number of birds observed per hour (average)	3–118 32.12	5–46 17.55	28.82	21.42	323.66	71.66	82.54
Number of species observed	20 Av. 10.5	15 Av. 5.8	11 Av. 7.5	13 —	15 Av. 7.5	13 Av. 6.6	37 Av. 8.5

decrease of *O. furcata* was recorded, but whether *leucorhoa* dominates *furcata* is not certain. It is to be added that on June 11, all of the birds (*O. leucorhoa*) were steadily moving eastward, which suggested a migration out of the most suitable temperature zone in accordance with some oceanic conditions. Thus, the range of temperatures recorded for *leucorhoa* was much greater than for *furcata*, while *O. castro* was distinctly a warm current species.

	O. furcata	*O. leucorhoa*	*O. castro*
Air temperature, °C.	5–11.5 Rarely 12–14 A straggler at 21	3.5–22 Mostly 7–15 Especially 13–15	16.5–22.5
Water temperature, °C.	3–8 Once 11 A straggler at 15.5	2.3–16 Especially 6–8	10.8–16 Rare at 8

THE SHEARWATERS AND FULMARS: *Puffinus tenuirostris* and *P. griseus* showed distinct segregation to cold and warm currents respectively. The former was one of the commonest species in the northern seas, though it was rare off the Kuriles, but it was again found mixed with numerous *griseus* in warmer Japanese waters. The latter species was never found in the cold waters except for a few off Kushiro east of the convergence, but it was not seen on the offshore true warm current surface. Other migrant southern hemisphere species, and the fulmars and the Japanese streaked shearwater (*Calonectris leucomelas*), preferred the following temperatures.

	AIR TEMPERATURE °C.	WATER TEMPERATURE °C.
Puffinus tenuirostris	6–11.5 A few 17–20	3.5–7 A few 14.8–15
P. griseus	17–20 A few 7	11.2–12.5 A few 8.2
P. carneipes	16.5–20.7	10.8–16
P. bulleri	18.5–22.5	14.5–16
Calonectris leucomelas	19–20	12–12.5
Pterodroma solandri	12–22.5 Once 7	7.5–16 Once 6.2
Pt. inexpectata	6.2–9	5–6.2
Fulmarus glacialis	6–11.5 A few 17–20	3.5–7 A few 14.8–15

Synthliboramphus wumizusume was distinctly restricted to the warm currents, unlike all of its relatives, which are cold current birds. *Catharacta skua*, from the cool waters of the southern hemisphere, also was restricted to the warm current surface in this sea zone, while the arctic breeding skuas were found in cold currents, except for three individuals which were migrating across the warm current waters.

SUMMARY

1. During a research cruise from Japan to the west Bering Sea, June to July, 1954, a sea bird census was made.

2. As an indication of population density, the number of birds observed per hour was used. The speed of the ship averaged 7 miles per hour, and the number of birds per square mile was calculated for sample sea divisions.

3. Attempts were made to show a correlation of bird density with food supply.

4. Distribution of sea birds is subject to zoogeographic factors (endemism) and to ecological factors (food and temperature), as well as to seasonal physiological cycles and movements. Sea zones were divided according to air and water temperatures and to relative abundance of sea birds.

5. The distribution pattern was different for different species of sea bird. Flocking species, although generally distributed, showed a clustered pattern, concentrating where food was abundant, while solitary species were distributed at random, since sparse amounts of food suffice for them.

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A Survey for Alkaloids in Hawaiian Plants. II

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WITH PART I[3] of this series a systematic survey for alkaloids in Hawaiian plants was initiated. This paper reports tests on 29 additional species as well as tests on different plant parts from 18 of the species covered by Part I.

All of the specimens tested were collected from living plants on the island of Oahu except for one, *Curcuma xanthorrhiza*.

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[3] In Pacific Sci. 13(3): 295–305.

METHODS

The testing methods devised for this survey have already been described (Swanholm *et al.*, 1959). The only modification in the testing procedure involves the extraction technique.

EXTRACTION OF PLANT MATERIAL. About 2–5 grams of the plant material was pulped in a Waring blender with 100 ml. water for 5–10 minutes. The plant slurry was transferred to an Erlenmeyer flask and 5 ml. of concentrated hydrochloric acid were added. The slurry was digested on a hot plate at about 80° C. for 6–12 hours. The cooled slurry was filtered through fine paper and 0.2 ml. of the filtrate was used in each test.

The information obtained by digesting with Prollius' fluid appeared insufficient to warrant its continued use.

KEY TO ABBREVIATIONS IN TABLE 1

The results of the spot tests are given in the following order and abbreviated form:

BINOMIAL	The accepted botanical name. The authority is omitted to conserve space. An asterisk (*) indicates introduced species.
LOCAL NAME	The Hawaiian or vernacular name, if known.
LOCALITY	The nearest town or other prominent map feature.
DATE COLLECTED	Date of actual collection in the field.
DATE TESTED	Date of actual application of spot tests.
PLANT PART(S)	B—bark, Br—branchlet, F—fruit, Fl—flower, H—herb or whole plant, L—leaf, R—root or underground part, RB—root bark, S—seed, St—stem, W—wood, I—immature, M—mature.
ALKALOID REAGENTS	M—Mayer's, P—Picric Acid (Hager's), I—Iodine (Wagner's), D—Dragendorff's, S—Sonnenschein's, T—Silicotungstic Acid.
PRECIPITATES	The precipitates from the hydrochloric acid extract are classified on a tr (trace), + (light), ++ (heavy) basis. A — indicates no precipitation and a ? indicates that the test was meaningless.

TABLE 1

RESULTS OF SPOT TESTS FOR ALKALOIDS
(Plants are listed alphabetically within each taxon.)

BINOMIAL	LOCAL NAME	LOCALITY	DATE COLLECTED	DATE TESTED	PLANT PART(S)	ALKALOID PRECIPITATES	COMMENTS
APOCYNACEAE							
Pteralyxia macrocarpa	Kaulu	Pupukea–Kahuku Road, Oahu	27 Jan 58	19 Feb 58	B	S+,D+,I+ M—,T+,P?	Endemic genus of two species
					RB	S+,D+,I+ Mtr,T+,P+	
					Trunk Heartwood	S+,D+,Itr M—,Ttr,P—	
					Root Heartwood	S—,D—,I— M—,T—,P—	
					L	S++,D++,I++ M+,T++,P+	
ARACEAE							
*Colocasia esculenta**	Taro, Kalo	Waiahole ditch trail, Oahu	27 Jan 58	19 Feb 58	H	S+,Dtr,I— M—,T++,P—	Aboriginal introduction, cultivated specimen
BORAGINACEAE							
*Cordia subcordata**	Kou	UH campus, Oahu	23 Jan 58	24 Jan 58	B,Fl, L,St	S+,D—,I— M—,T+,P—	Aboriginal introduction, cultivated specimen
CELASTRACEAE							
Perrottetia sandwicensis	Olomea	Pupukea trail, Oahu	15 Jun 58	18 Jun 58	Br,R	S+,D—,I— M—,T+,Ptr	Endemic species
COMPOSITAE							
Hesperomannia Swezeyi	—	Pupukea trail, Oahu	18 Jun 58	20 Jun 58	L,R,St	S++,D+,I— Mtr,T++,P—	Endemic genus
CYATHEAE							
Cibotium Chamissoi	Hapu'u-'i'i	Pupukea trail, Oahu	2 Mar 58	8 Mar 58	Fronds,St, Tubercles	S+,Dtr,Itr M—,T+,P—	Endemic tree fern
C. splendens	Hapu'u	Pupukea trail, Oahu	2 Mar 58	8 Mar 58	Fronds,St, Tubercles	S++,Dtr,I— M—,T++,P—	Endemic tree fern
EUPHORBIACEAE							
Euphorbia Rockii	'akoko	Pupukea trail, Oahu	2 Mar 58	5 Mar 58	Fl,L,R,St	S+,D—,I— M—,T+,P—	Endemic species

TABLE 1 *Continued*

BINOMIAL	LOCAL NAME	LOCALITY	DATE COLLECTED	DATE TESTED	PLANT PART(S)	ALKALOID PRECIPITATES	COMMENTS
GESNERIACEAE *Cyrtandra brevicalyx*	Pioha	Pupukea trail, Oahu	15 Jun 58	18 Jun 58	B,Br,R	S+,D+,Itr Mtr,T+,P—	A genus of 130 Hawaiian species
C. leucocalyx	Kanawaoke'oke'o	Pupukea trail, Oahu	15 Jun 58	18 Jun 58	L,R,St	S+,D+,I— Mtr,T+,Ptr	Endemic species
GOODENIACEAE *Scaevola mollis*	Naupaka-kuahiwi	Pupukea trail, Oahu	18 Jun 58	20 Jun 58	B,Fl,L,R,St	S++,D+,I+ M+,T++,Ptr	Endemic species
LEGUMINOSAE *Caesalpinia pulcherrima**	Pride of Barbados, 'ohai-ali'i	UH campus, Oahu	23 Jun 58	24 Jun 58	B,F,Fl,L,St	S++,Dtr,I— M—,T++,P—	Cultivated specimen
LILIACEAE *Cordyline terminalis**	Ti, Ki	UH campus, Oahu	23 Jun 58	24 Jun 58	B,L,R,St	S—,Dtr,Itr M—,Ttr,P—	Aboriginal introduction, cultivated specimen
LOBELIACEAE *Clermontia persicaefolia*	'oha-wai	Pupukea trail, Oahu	15 Jun 58	17 Jun 58	B,L,R	Str,D—,I— M—,Ttr,Ptr	Endemic genus
			18 Jun 58	21 Jun 58	B,L,R	S++,D+,I+ Mtr,T++,Ptr	Different specimen from above
Cyanea sp.	'oha, 'oha-wai	Pupukea trail, Oahu	2 Mar 58	8 Mar 58	L,R,St	S+,D+,I+ M+,I+,P+	Endemic genus
MALVACEAE *Hibiscus tiliaceus**	Hau	UH campus, Oahu	23 Jun 58	24 Jun 58	B,L,R,St	S+,Dtr,I— M—,T+,P—	Aboriginal introduction from tropical Asia, cultivated specimen
MORACEAE *Artocarpus incisus**	Breadfruit, 'ulu	UH campus, Oahu	23 Jun 58	24 Jun 58	B,F,L,R,St	S++,D+,I+ M—,T+,P—	Aboriginal introduction from Guam, cultivated specimen
MYRSINACEAE *Myrsine sandwicensis*	Kolea-lau-li'i	Pupukea trail, Oahu	15 Jun 58	17 Jun 58	L,St	Str,D—,I— M—,Ttr,P—	Endemic species

PALMAE							
Pritchardia Hillebrandi	Loulu-lelo	UH campus, Oahu	23 Jun 58	24 Jun 58	R,St	Str,D—,I— M—,Ttr,P—	Endemic to Molokai Island, cultivated specimen
POLYPODIACEAE							
Grammitis tenella	—	Pupukea trail, Oahu	2 Mar 58	8 Mar 58	H	S—,D—,I— M—,Ttr,P—	Endemic species
RUBIACEAE							
Gardenia Mannii	Nanu, Na'u	Pupukea trail, Oahu	2 Mar 58	8 Mar 58	Br,L,St	S+,D++,I+ M+,T++,P++	Endemic to Oahu
			15 Jun 58	17 Jun 58	R	S+,D+,Itr Mtr,T+,Ptr	
RUTACEAE							
Fagara semiarticulata	Kawa'u, Hea'e	Pupukea trail, Oahu	15 Jun 58	17 Jun 58	Fl,L,R,St	S++,D++,I++ M++,T++,P++	Endemic species
				18 Jun 58	ML	S++,D++,I++ M++,T++,P++	
					Trunk Heartwood	S+,D+,I+ Mtr,T+,Ptr	
Pelea sandwicensis	Alani	Pupukea trail, Oahu	15 Jun 58	17 Jun 58	L,R,St	S++,Dtr,Itr M—,T++,Ptr	Endemic species
					F,Fl	S++,Dtr,I— M—,T++,Ptr	
Platydesma campanulata	Pilo-kea	Pupukea trail, Oahu	2 Mar 58	5 Mar 58	L,R,St	S++,D++,I++ M++,T++,P++	Endemic genus of 3 species
			18 Jun 58	21 Jun 58	B,L,R	S++,D++,I++ M++,T++,P++	
P. cornuta	Pilo-kea-lau-li'i	Pupukea trail, Oahu	2 Mar 58	5 Mar 58	L,R,St	S++,D+,I+ Mtr,T++,P+	
SAPINDACEAE							
Sapindus oahuensis	'aulu, lonomea	Kealia trail, Oahu	18 Mar 58	20 Mar 58	MF,L,St	S++,D++,I— M—,T++,P—	Endemic to Oahu

TABLE 1 *Continued*

BINOMIAL	LOCAL NAME	LOCALITY	DATE COLLECTED	DATE TESTED	PLANT PART(S)	ALKALOID PRECIPITATES	COMMENTS
Sapindus oahuensis		UH campus, Oahu	20 Mar 58	21 Mar 58	B,R	Str,D—,J— M—,Ttr,P—	Cultivated specimen
SAPOTACEAE							
Planchonella sp.	ʻala'a	Pupukea trail, Oahu	15 Jun 58	17 Jun 58	B,Br	Str,Dtr,J— M—,T+,Ptr	Different from *P. sandwicensis*
SAXIFRAGACEAE							
Broussaisia arguta	Kanawao	Pupukea trail, Oahu	2 Mar 58	8 Mar 58	Br,R	Str,D—,J— M—,T+,P—	Endemic genus of 2 species
ZINGIBERACEAE							
Curcuma xanthorrhiza[a]	—	Indonesia	—	16 Mar 58	R	S—,D—,J— M—,T+,P—	Native to Indonesia

RESULTS AND DISCUSSION

Table 1 lists the results of the alkaloid tests which were carried out on 29 plant species, representing 26 genera and 23 families. The 5 species which gave positive tests (+ or ++) with all six reagents are listed in Table 2.

Table 3, which supplements Part I of this series, lists the results of the alkaloid tests which were carried out on 18 plant species, representing 16 genera and 13 families.

Results from Part I are included with the present results in the following analysis.

To date, 125 plant species, representing 94 genera and 57 families, have been tested for alkaloids. This constitutes approximately 10 per cent of the native Hawaiian flora.

It is worth noting that the endemic genus *Straussia* has given quite variable results even among specimens of the same species. This variability would suggest that a botanical revision of this genus is in order.

TABLE 2

SPECIES GIVING POSITIVE (+ OR ++) TESTS FOR ALKALOIDS

BINOMIAL	FAMILY	PLANT PART(S) TESTED
Cyanea sp.	Lobeliaceae	Leaves, Root, Stem
Fagara semiarticulata	Rutaceae	Leaves, Flowers, Root, Stem
Gardenia Mannii	Rubiaceae	Branchlet, Leaves, Stem
Platydesma campanulata	Rutaceae	Leaves, Root, Stem
Pteralyxia macrocarpa	Apocynaceae	Leaves

TABLE 3

SPECIES RE-EXAMINED FOR ALKALOIDS[1]

(Plants are listed alphabetically within each taxon.)

(For KEY TO ABBREVIATIONS, see Table 1)

BINOMIAL	LOCAL NAME	LOCALITY	DATE COLLECTED	DATE TESTED	PLANT PART(S)	ALKALOID PRECIPITATES	COMMENTS
APOCYNACEAE *Alyxia olivaeformis*	Maile	Pupukea trail, Oahu	18 Jun 58	20 Jun 58	IF	Str,D—,I—,M—, T—,P—	Endemic species
ARALIACEAE *Tetraplasandra* sp.	Ohe	Pupukea trail, Oahu	2 Mar 58	5 Mar 58	B	Str,Dtr,Itr,Mtr, Ttr,P?	Endemic genus
COMPOSITAE *Dubautia plantaginea*	Na'ena'e	Pupukea trail, Oahu	18 Jun 58	21 Jun 58	B,L,R	S++,D++,I+, M—,T++,Ptr	Endemic genus
EUPHORBIACEAE *Antidesma platyphyllum*	Ha'a, Hame	Pupukea trail, Oahu	18 Jun 58	20 Jun 58	B,L,R	S+,D+,Itr,Mtr, T+,P—	Endemic species
LILIACEAE *Smilax sandwicensis*	Hoi-kuahiwi	Pupukea trail, Oahu	2 Mar 58	8 Mar 58	R	Str,Dtr,I—,M—, T+,P—	Endemic species
LOBELIACEAE *Cyanea angustifolia*	'oha-wai, 'oha	Pupukea trail, Oahu	18 Jun 58	21 Jun 58	B,L,R	S++,D++,I++, M++,T++,P++	Endemic genus
MYRSINACEAE *Myrsine Lessertiana*	Kolea-lau-nui	Pupukea trail, Oahu	2 Mar 58	5 Mar 58	B,Fl,R	S—,D—,I—,M—, Ttr,P—	Endemic species
OLEACEAE *Osmanthus sandwicensis*	Olopua	Pupukea trail, Oahu	15 Jun 58	17 Jun 58	B,RB,L	S+,D+,Itr,M++, T+,Ptr	Endemic species
PALMAE *Pritchardia* sp.	Loulu	Pupukea trail, Oahu	15 Jun 58	17 Jun 58	L,St	Str,D—,I—,M—, Ttr,P—	Endemic species
RUBIACEAE *Canthium odoratum*	Walahe'e, alahe'e	Kealia trail, Oahu	18 Mar 58	20 Mar 58	R	S+,D—,I—,M—, T+,P—	Indigenous, but widespread

[1] This table lists the results of alkaloid tests on other plant parts than those which were presented in Part I of this series (Swanholm *et al.*, 1959).

TABLE 3 *Continued*

BINOMIAL	LOCAL NAME	LOCALITY	DATE COLLECTED	DATE TESTED	PLANT PART(S)	ALKALOID PRECIPITATES	COMMENTS
Gouldia terminalis	Manono	Pupukea trail, Oahu	15 Jun 58	17 Jun 58	B,L,Fl,St	S++,D+,Itr,M—, T++,P—	Endemic genus
*Morinda citrifolia**	Noni, Indian mulberry	Waiahole ditch trail, Oahu	22 Feb 57	20 Mar 57	MF	S+,D+,I—,M—, T+,P—	Aboriginal introduction
Straussia kaduana	Kopiko-kea	Pupukea trail, Oahu	18 Jun 58	20 Jun 58	B,L,R	S+,Dtr,I—,M—, T+,P—	Endemic genus
S. Mariniana	Kopiko	Pupukea trail, Oahu	15 Jun 58	17 Jun 58	L,St	S+,Dtr,Itr,M—, T+,Ptr	Tests within this genus have been inconsistent
RUTACEAE							
Pelea clusiaefolia	Alani	Pupukea trail, Oahu	2 Mar 58	5 Mar 58	R	Str,D—,I—,M—, Ttr,P—	Endemic species
P. Waianaeana	Alani	Pupukea trail, Oahu	18 Jun 58	20 Jun 58	IF,MF	Str,D—,I—,M—, T—,P—	Endemic species
					B,R	S+,D—,I—,M—, Ttr,P—	
					ML	S++,Dtr,I—,M—, T++,Ptr	
TACCACEAE							
*Tacca Leontopetaloides**	Pia	UH campus, Oahu	1 Dec 57	19 Feb 58	Petiole	S—,D—,I—,M—, T—,P—	Aboriginal introduction, cultivated specimen
THYMELAEACEAE							
Wikstroemia oahuensis	'akia	Pupukea trail, Oahu	2 Mar 58	8 Mar 58	L,St	S+,D+,Itr,M—, T+,P—	Endemic species

Lord Howe Island, a Riddle of the Pacific. Part II

S. J. PARAMONOV[1]

IN THE FIRST PART of this work (Paramonov, 1958), the general features of this island were dealt with. Now a summary of our knowledge about the fauna of the island is given. We will discuss the different groups separately.

MAN

Up to the present date no trace of aboriginal man has been found on the island, which indicates that the isolation of the island was very strong, and that it was not part of a sunken continent once inhabited by man. Probably even the canoes of Polynesian people never visited this island, because once being visited it would have been populated, as excellent conditions exist there for maintaining human life.

MAMMALIA

There are practically no mammals in the natural fauna of the island. Only some bats are reported: the little brown bat (*Vespadelus pumilus* Gray), and *Scotophilus morio* Gray = (*Chalinolobus tuberculatus* Forst.). Doubtless more species of migrating bats occur on the island but they have not yet been recorded, or have been recorded (for example, the flying fox) without support of preserved specimens. In any case, there are no endemic species of bats on the island, and there is no ground for expecting them. Generally these animals are rare on the island. Etheridge (1889) wrote: "We anticipated meeting with bats in the coral-rock caves at North Bay, one of the most favourable habitats for them on the whole island, but not the slightest trace was found." This statement is good evidence of the rarity of the bats.

The introduced mammal fauna consists now of rats, mice, goats, and pigs. The first two are practically domesticated, the latter two live in the wild state in the two high parts of the island, separated by the intermediate low land occupied by man.

The absence of mammals indicates that the island was not part of a continent, otherwise the Australian marsupials would be represented in the island fauna.

AVES

The Extinct Birds

1. The white swamp hen, *Notornis* or *Porphyrio albus* Gray, the most famous of the extinct Lord Howe Island birds:

E. S. Hill, in 1870, wrote: "With the exception of the skin in the Imperial collection at Vienna, there appears to be only one other in existence, which is said by Prof. A. Newton to be in the Derby Museum at Liverpool." Several original drawings are in existence, all made soon after the discovery of the island. From these paintings we learn that the species when young was entirely black, becoming bluish grey and finally entirely white with maturity. Some of the adult birds were tinged with blue, especially on the wings. Probably sexual difference was responsible for the different appearance of the birds. The feathers of the neck and breast possessed a yellowish tinge, those of the remainder of the body had a delicate indication of blue. The legs were yellow, the bill, forehead, and the iris of the eyes red.

This bird appears to have been first mentioned by Callam in 1783, and afterwards in "Phillip's Voyage to Botany Bay," (1789: 160), and again under the name of *Gallinula alba*, by White in his "Voyage to New South Wales" (1790: 238). Further mention of this bird will be found in von Pelzeln's paper, in "Ibis" (1871: 44), where its relationship to the genus *Notornis* was first pointed out; also a good figure of it will be found in "Ibis," 1873, pl. 10.

The genus *Notornis* is present in New Zealand, but is quite absent from Australia. This fact, however, does not speak in favour of a

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New Zealand origin of the species from Lord Howe Island, because on the mainland this fearless bird, which is also a poor flier, can be very easily destroyed. Only a few decades of the presence of man on the island was enough to cause the complete extinction of this bird. On the mainland it would have been practically helpless, therefore we cannot reject the idea that this genus was not also represented in the past on the mainland.

The presence on the island of a bird which is a poor flier suggests a continental origin of the species.

2. The Lord Howe Island pigeon, *Janthoenas godmanae* (Mathews):

This bird was larger than a domestic pigeon, its head and breast were of a purple-mauve tint, its throat was white, and the mantle or back of the neck was green, the rest of the body being brown. The Lord Howe Island pigeon was once so numerous and tame that, with the aid of a stick and string, the islanders could snare 20 birds from a flock without the others taking alarm. Surgeon Bowes and others, in 1788, merely knocked them over with sticks. Today there is not a skin in any museum in the world, and only two paintings are known, one dated 1790 and signed by George Raper, and the other, unsigned, in the Alexander Turnbull Library, Wellington, New Zealand. Several related species occur in New Caledonia, New Guinea, Timor, and other places. The species appears to have been exterminated about 1850.

3. The Lord Howe Island parrakeet, *Cyanorhamphus novaezeelandiae subflavescens* (Salvadori):

In size it was somewhat smaller than a Rosella parrot, and was mostly bright green in colour, with patches of red on the forehead, sides of neck, and rump, and blue on the wings. A single pair was seen flying through the forest in 1869 (Hill: 1870). The species existed until about 1870, by which time it had been exterminated because of the damage it did to the crops of the settlers.

Birds very closely related to the Lord Howe Island parrakeet still exist on Norfolk Island, New Caledonia, New Zealand, and some associated islands.

The Present Land Birds

Very rare, curious, and stupid is the so-called wood hen, *Ocydromus* (*Nesolimnas*) *sylvestris* Sclat. Its plumage is of a brown colour tinged with green, which harmonises well with the dark-brown earth and the green foliage of the palm scrub in which it wanders about, turning over leaves and pebbles with its long grey bill, in search of food. The wood hen's wings are so small that it cannot fly but its strong legs have enabled it to ascend, for example, even the steep faces of Mount Lidgbird.

The bird deserves full protection because its curiosity is very strong, and to attract it and catch it one only needs to pick up pebbles and to tap them upon a tree trunk or a rock. McCulloch, 1921, writes: ". . . we saw the birds hastening towards us. Espying us within thirty yards or so, they advanced more cautiously, but, if we remained still, approached sufficiently close to be snared with a palm-leaf noose. I tethered one by the leg to a stone in order to take its photograph, and its efforts to escape attracted the attention of another which endeavoured to assist the captive by grasping its neck with its own long bill and pulling with all its strength."

These birds are now to be found only on the upper parts of the two mountains and in such inaccessible places as the Big and Little Slopes beneath the southern cliffs of Mount Gower. The only protection for this bird is its isolated habitat.

It is now the most remarkable animal of the island, and the duty of the islanders is to protect it by all means. First of all it is necessary to proclaim its *absolute* protection, only photography being permitted to visitors, and to impose a heavy penalty for breach of the proclamation.

The ouzel or doctor bird, *Turdus xanthropus vinitinctus* Gould, is another rarity. The general colour of this bird, which is thick set and some 9 inches in length, is a dark reddish brown. The vinous-tinted ouzel belongs to a large group of birds which includes the missel thrush, song thrush, and blackbird of England (the last one is introduced in Australia and New Zealand). Its nearest relative is a form living in New Caledonia. The genus is represented by species on most of the islands of the western Pacific, but

is absent from Australia. Hindwood (1938) regarded it as an extinct bird.

The Lord Howe Island starling, *Aplonis fuscus hullianus* Gould, is similar in size to the ouzel. It is blackish brown in colour, glossed with bottle green, the underparts being olive grey. Its nearest relative is a subspecies existing on Norfolk Island. It belongs to the genus with a wide distribution throughout the islands of the western Pacific. Hindwood (1938) regarded it as an extinct species.

Concerning the robust silver-eye, *Nesozosterops strenua* Gould, Hindwood (1938) wrote: "Until recently there existed on the island a big silver-eye, about half as large again as the grey-backed species at present living on Lord Howe Island. Birds similar to the now extinct robust silver-eye occur on Norfolk Island (2 species) and in the Solomons (1 species)." The author considers that the extinction of robust silver-eye needs to be confirmed.

The Lord Howe Island flyeater, *Gerygone insularis* Ramsay, is also called the "rain-bird" because it was active after rain, or the "pop-goes-the-weasel" on account of the supposed resemblance of its song to that air. It is the smallest of the birds on the island, and belongs to a group with a wide distribution in Australia, New Guinea, the Pacific islands, and New Zealand. Hindwood (1938) regarded this species as extinct.

The author is not quite sure that the data of Hindwood are correct. In 1955 and 1956, when the author visited the island, he saw *Gerygone insularis* as a rather common bird, although this species was regarded by Hindwood as extinct. It seems that some species were rare in 1938, but were not entirely exterminated. In 1955–56 the author found very good conditions for life of the birds: there were no wild cats, no wild dogs, very few rats; if from time to time some specimens of these animals destroy birds, the number of victims is probably very small. Again, man is not now interested in destroying birds. The evidence is that on the first day of arrival the author's assistant caught a ground pigeon by hand (after examination it was liberated); the author himself made attempts to catch this bird with an entomological net in the courtyard of the Guest House. If this bird is so fearless, lying on its side on the ground, it is quite evident that conditions on the island are now such as to account for this.

Of the Lord Howe Island fantail, *Rhipidura flabellifera cervina* Ramsay, Hindwood (1938) wrote: "This bird was an insular form of the well-known grey fantail of Eastern Australia. It was exceedingly tame and would often enter dwellings and capture flies."

Introduced Birds

According to Hindwood (1938), "the grey-breasted silver-eye, *Zosterops lateralis* (Latham), was in danger of being exterminated, but a number of birds of the Australian race, and the Norfolk Island form as well, were introduced in 1924 and 1925, with the result that it appears to be increasing."

The author saw some silver-eyes during his visit to the island in 1955. The future naturalist must consider the fact that some birds were introduced. According to Hindwood, "certain introduced birds such as the Californian quail and the land rail have also been exterminated by the rats."

Another passage of Hindwood is interesting: "In an effort to check the increase of the rats almost one hundred owls of *several kinds* were sent to the island between 1922 and 1930." However, only *Ninox boobooc* Latham, which existed before the invasion of the rats, is now living on the island.

The number of rats destroyed is very interesting: in the year 1927, 13,771; in 1928, 21,214; in 1929, 10,175; in 1930, 17,803. These figures must represent but a small proportion of the total rat population, so it is difficult to understand how the whole bird population of the island was not totally destroyed, for rats can climb the trees and very easily destroy eggs and nestlings. Probably the high mountain areas served as sanctuaries for the birds. Now (1955–56) the rats are common only around dwellings of humans. During the five weeks the author was on the island he saw very few rats in the bush either on day or night trips.

According to M. Nicholls (1953) "the land rails liberated on the island about 1880 were supposed to have succumbed to the rats, but in February 1944, several were observed in a drain

at Robbin's Farm." Probably the land rails survived the rat invasion but, not being very numerous, escaped observation.

REPTILIA

The fauna of reptilia is extremely poor. Corrie (1878) stated wrongly that neither snakes nor lizards are known on the island; snakes are certainly unknown, but three species of *Lacertilia* are present.

There are two species of Geckonidae: *Phyllodactylus guentheri* Boulanger and *Gehyra oceanica* Grey. The first is also known to exist both on Norfolk Island and in northwest Australia, the second appears to be generally distributed throughout the South Pacific islands. The distribution of geckos is usually connected with the transportation of various tropical fruits in bunches, in which they often hide. More interesting from the zoogeographical point of view is the presence of the third species, *Lygosoma lichenigerum* O. Shaun. (Scincidae). The three species are also distributed on Rabbit (Goat) Island and the Admiralty Islets. They may be sought on dry stony ground, under stones, amongst dry leaves, and at the feet of low scrubby trees.

Of water chelonians there is no trace. Turtles are, however, known to frequent occasionally the shores of the island. In the early decades of the last century they were very numerous.

AMPHIBIA

Frogs, etc., are quite absent. The absence of amphibians may be connected with the absence of permanent fresh-water pools on the island.

The Evertebrata will be discussed in some detail later.

FRESH-WATER FAUNA

The fresh-water fauna of the island is very poor, but interesting. The poverty of this fauna can be easily explained by the absence of large permanent streams or water pools. In each large valley there are streams but they are not truly permanent. One of the bigger streams is situated at northern part of the settlement, but its estuary is usually filled with salt water which enters during high tide and extends rather far inland. There are also some isolated lagoons, but their fauna was not studied regularly.

However, there are some species with extremely peculiar distributions. For example, under stones in the several streams, anywhere from sea level, as in the Big Creek, to the mountain tops, there is living a tiny fresh-water crab, *Hymenosoma lacustris*. This species is the only fresh-water representative of a common marine genus. It was first recognised in New Zealand, later it was found in landlocked lakes in Victoria, Australia, and afterwards at Lord Howe and Norfolk islands. Its permanent associate is a fresh-water prawn, a *Paratya* (*Xiphocaris*) species.

How is it that these species appear in fresh water in such widely separated localities? It might be supposed that they spend some of their earlier stages in the sea and that later some individuals have drifted from one locality to another. However, this suggestion is discounted by the fact that they occur in landlocked lakes, and on Lord Howe Island on the top of Mt. Gower, to which access from the sea is impossible because the streams from the top disappear before they reach sea level.

We could suggest that the crab and the prawn are survivors of an ancient fauna which passed from one place to another by means of old land connections, long since disappeared. But this explanation is also unsatisfactory, because we must suppose a land mass including Victoria, Norfolk Island, Lord Howe Island, and New Zealand and the commonest animals and plants of all the above-mentioned areas are not preserved on Lord Howe Island.

Again, we could imagine also that the eggs were transported upon the feet of wading birds, but if so, why do these crabs and prawns not live in all the lakes of Australia, but only in some of them in Victoria?

It is necessary to add that in addition to the crabs and prawns there are tiny eels (*Anguilla*). Their occurrence on the summit is more easily explained, for young eels can migrate for considerable distances along streams and over moist surfaces. Although their occurrence on the summit can be accepted it is not possible to imagine where they would find conditions suitable for development to maturity.

Thus, the distribution of these animals is mysterious. R. Etheridge, Jr. (1889: 32) also

recorded a specimen of water scorpion, *Belostoma indicum* Les., the presence of which on so isolated an island is not easy to explain.

THE RECENT HISTORY OF THE FAUNA

In order to understand the composition of the fauna it is necessary to know what elements of the fauna have arrived on the island with man (since about 200 years ago). Therefore, we will trace the most important moments in the recent history of the island.

The island was discovered by Lieutenant Lidgbird Ball on 17 Feb. 1788, but the first landing took place on 13 March 1788. Ball has written in his journal: ". . . sent a boat to examine the isle, and found abundance of turtle. . . ." The next notice on 14 May 1788: "Hoisted the jollyboat out and sent her on shore."

Gilbert noticed in his journal on 16 May: ". . . he (Capt. Ball) informed me that the island afforded plenty fine turtles, fowls, fish, coconuts and cabbages," and further:

At the head of the bay grew a fine long grass, and the whole island appeared to be covered with trees, among which mangroves and coconuts were conspicuous. There was a very thick undergrowth of a vine resembling ratten, which crept along the ground and greatly impeded us in the pursuit of birds. The surface of the island in centre was composed of sea sand, mixed with marine shells, and most parts were covered with trees. The island seemed to be about 16 miles long. Great numbers of gannets, very large and fat, were about, showing less fear than geese in a farmyard. We found many nests in the long grass at the head of the bay. On entering the woods I was surprised to see large fat pigeons of the same plumage and shape as those in Europe. They were so tame as to be knocked down with little trouble. Partridges, likewise, in great numbers ran along the ground. Several of these I

FIG. 1. Lord Howe Island. The mountainous southern part of the island as seen from northwest. At right Mt. Gower, at left Mt. Lidgbird. In foreground, Rabbit Island. The slopes of both mountains are densely afforested. Photo: Miss Zenta Liepa.

knocked down and placed near me as I sat under a tree. Five or six dozen of the same kind came up, and I was able to take nearly the whole lot. The only traces of people we saw were those made by the 'Supply's' crew when they were first here. Among the different kinds of birds we met were some as big as a large fowl, and quite white. They had long yellow legs and a very strong red beak. I caught six of these by running them down among the low bushes. The cock birds were very beautiful; their white feathers were tinged with azure blue. I saw also several birds that were not unlike peacocks, but caught none of them. At noon I returned to the beach and found the crew had collected cocoanuts, cabbages, birds, and a great quantity of fish.

From these reports it is quite evident that the landings were very short and that nothing was transported ashore. From 1788 to 1830 there is not much information available, with only whaling vessels probably stopping there to get wood and water.

In 1833 or 1834 the first actual settlement was made: three white men, two women, and two Maori boys. After several years' stay the whole party returned to New Zealand. These first settlers had the opportunity to transport some domesticated animals to the island.

The first survey was done by H. J. White, 1835 (report of 1853); in the report we can read: "There are residing on the island four men, three N. Z. women and two children, subsisting upon birds and fish, which are caught in great abundance."

In the report from 1853, Capt. Denham writes that since 1843 three families (total community 16 people) cultivated 44 acres on the island. This was practically a second colonisation, this time from the mainland of Australia.

Dr. Foulis in his report of 1851 states: ". . . sixty to 80 whaling vessels per year have called for provisions. . . ."

M. Nicholls (1938–1953) in the different editions of his history of Lord Howe Island gives a lengthy report about vessels visiting the island from 1788 to 1949.

The development of culture on the island since 1788 has had a very slow progressive destroying influence on the native fauna, but in 1918 there was a calamity which changed the whole face of the original fauna: in 2–5 years it became very poor and uniform, and many species of animals, including insects, became extinct.

On 14 June 1918, the vessel "Makambo" struck a rock in the area of Admiralty Islands. Many cases of fruit and tons of copra were thrown overboard and this was the means by which rats got ashore. It was a tragedy especially for the birds. Within two years this paradise of birds had become a wilderness, and the quiet of death reigned where once all was melody.

After a few months' time rats began to visit the houses and soon spread over the whole island, even to the tops of the mountains, destroying all that was edible. The smaller land birds soon disappeared and then it was found that the rats were attacking the palm seeds, which were at that period the basis of the most important industry of the island.

A bonus of 6d a tail was paid for several years, but was reduced later to 4d per tail. For the year 1936 about 20,000 tails were handed in. At the present time rats are not rare on the island, but their numbers have been reduced to an acceptable level. However, this was too late. The destruction of the birds was terrific, and their recovery from the rat invasion has been very slow.

Another factor changing the fauna, although not directly, was the presence of wild goats and pigs. The year when goats were first brought to the island has not been recorded, but it must have been at a very early date, probably around 1830. The damage caused by these animals was not very extensive, but the pigs, destroying the roots of some plants, are suspected by botanists to be the cause of the great rarity (and probably extinction) of some plants. Naturally, with the destruction of the plants, those animals biologically closely connected with them were destroyed too.

Today the goats and pigs do not play an important role. They are very shy and avoid the presence of man as much as possible.

It is necessary to note that the fauna does not have a strictly permanent character. From time to time some animals, especially water birds, visit the island and stay some time, for example, one species of parrot, the Indian turtle dove, black swan, crow, etc., but sooner or later, gen-

FIG. 2. Mount Gower. Showing the nearly vertical slope and type of vegetation along the shore. Photo: Miss Zenta Liepa.

erally after the presence of only some months, they disappear (for more details see M. Nicholls, 1953).

It is evident that the niches on the island suitable for them are too small for their survival.

THE MAIN GOAL OF THE NATURALIST'S EXPLORATION

The most interesting parts of the island, the summits of Mt. Lidgbird and Mt. Gower, are practically unexplored. Only a few naturalists have reached the summits, and their visits were mostly of a tourist character. Nobody has stayed in these areas very long, visits usually being confined to only a few hours, so naturally we have a very insufficient and superficial knowledge of the fauna and flora, which are quite different from those of the lower part of the island.

Especially interesting is the summit of Mount Gower, which is very different from that of Mt. Lidgbird. The top of Mt. Gower is a comparatively flat area several hundred acres in extent, whereas the summit of Mt. Lidgbird consists practically only of slopes.

Two "runs" on the summit of Mt. Gower converge and disappear over the sheer cliffs, falling perhaps a thousand feet into the Erskine Valley. The water trickling down them is supplied direct from the clouds which so commonly envelop the mountain tops. Investigation of this area can produce extremely interesting data. For example, there is the record of a nymph of the family Peloridiidae (Homoptera), the species of which are distributed in Patagonia, Tierra del Fuego, New Zealand, Tasmania, and the eastern part of Queensland. The representatives of this family belong to the genus *Hemiodoecus* China: 2 species from Australia: *H. veitchi* and *H. wilsoni*, 2 species from Tasmania: *H. leai* and *H. fidelis*. *Xenophyes cascus* Bergr.

is distributed in New Zealand, and *Peloridium hammoniorum* Br. in Patagonia and Tierra del Fuego.

This area has a very humid atmosphere: mosses, lichens, and climbing ferns of many kinds cover the trunks of almost all the trees, while the ground is completely hidden under a thick growth of sphagnum. The tree fern, *Dixonia antarctica*, plays here an important role in the landscape.

Nobody has collected insects in light traps, or by other sorts of traps (carrion, fermented sugar juice, etc.). We can expect extraordinary results if these methods of collecting are used.

Another object for exploration is the so-called "Ball's Pyramid"—a pinnacle rising 1,800 feet into the sky, yet only a mile in circumference at its base (Fig. 4). It is located 11 miles to the southward (other data state 18 miles) from Lord Howe Island. Its upper slopes remain "terra incognita," as none but a few surveyors have ever landed upon the rocks around its base, and nobody has collected animals on this huge rock. It has some bushes, but exploration can be accomplished only with the help of alpinists' equipment. It is quite evident that some land birds can nest there, insects are also doubtlessly present, but they are absolutely unknown.

SOME USEFUL DATA FOR THE VISITING NATURALIST

Regular connection of Lord Howe Island with the mainland is maintained now only by flying boats (run by Ansett Airways), flying from Sydney one or two times a week. The flight takes about three and a half hours; in bad weather the flight is usually postponed till the weather improves. The flying boats land in the lagoon near a jetty, all passengers and their goods being transported to the jetty by motorboats. Thirty-

FIG. 3. Slopes of Mt. Lidgbird, showing the type of vegetation in the middle zone, about 800 feet above sea level. Photo: Miss Zenta Liepa.

FIG. 4. Ball's Pyramid, about 11 miles southeast of Lord Howe Island. The surface of this gigantic rock is unexplored. Its circumference is 1 mile, height 1,800 feet. Photo: R. Morris.

five pounds of luggage are carried free, cameras, binoculars, etc., not being included in the weight of the luggage. Excess luggage or freight costs 6d per pound.

On the island there are four hotels and guest houses with conditions similar to those on the mainland; some private houses also accommodate visitors (with full board). There is electric light. There are some privately owned trucks which can be used for transportation of heavy loads along the two or three main roads on the island. Bicycles are also available for hire for shorter trips on the island. There are three shops on the island in which the traveller can buy clothes, shoes, groceries, etc. Several tearooms serve refreshments and light meals.

Radio telegrams may be sent from any post office to the island or to any part of the Commonwealth from the island at 12 words for 2/6. The Commonwealth Savings Bank has an agency at the local post office. Visitors coming to the island can have their signatures forwarded by their own branches and can operate their accounts within certain limits laid down by the Head Office of the Bank.

Ordinary size films are available and a good developing and printing service is available at approximately city prices. There is no chemist's shop, but a small hospital and a dispensary is available; there is one doctor and a trained nurse.

Beer and spirits are now available on the island.

Professional guides for climbing the mountains are not available, but a number of experienced islanders are available for hire as mountain guides. Heavy loads can be transported by motorboats to areas nearer to the mountains.

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